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GENETICS OF LIVESTOCK IMPROVEMENT

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PREFACE

The purpose of this book is to outline the fundamental principles of animal breeding in as simple and practical a manner as possible. An attempt has been made to present the material both for the college undergraduate and for the practical animal breeder.

Animal breeding consists of three closely related fields: physiology of reproduction, genetics, and the application of genetics to the improvement of farm animals. The purpose here is not to cover in detail all three phases of this subject. Rather, the chief aim is to present the principles of genetics and their application. At times, however, some of the physiological aspects of animal breeding are included to clarify those of a genetic nature. This is especially true in the discussion of oögenesis and spermatogenesis.

The genetics of livestock improvement is the least understood of any phase of livestock production. One of the main reasons for this is that the science of genetics is relatively new. Mendel's classic paper on the basic concepts of inheritance was not discovered until about 1900, and only recently have these principles been applied in a practical way in plant and animal breeding. Another reason for the lack of understanding of the genetics of animal breeding is that new discoveries in this field have come more slowly than those in management, feeding, and disease control. Most discoveries in genetic research are not so spectacular as those in nutrition, for instance, where vitamins, antibiotics, and hormones have received much publicity in recent years and have been effective in increasing the efficiency of livestock production. Furthermore, new discoveries in genetics and animal breeding are usually difficult to apply, and their application often meets opposition from breeders as well as others. Last, but not least, the understanding of genetics is often difficult and requires considerable study; but no subject is more fascinating when the principles and their application are thoroughly understood.

During recent years, there has been an increase in the rate of application of genetics to the improvement of livestock production. Through the use of newly developed methods of breeding and selection, new strains used for the production of crossbred poultry have been formed and these crossbreds are much more productive and efficient than the breeds of a few years ago. The application of similar methods to swine production

has increased the rate and efficiency of gains in this class of farm animals. One of the main objectives of this book is to present these new findings and to explain how they might be applied to the breeding of better live stock in the United States.

The outline and much of the material used in this book has been derived from many semesters of teaching experience in this particular field. I take this opportunity to thank the many hundreds of students who have read and used parts of the manuscript in an animal breeding course and *have suggested points that needed to be expressed more clearly*. They also were diligent, at my request, in finding errors in the text. I also wish to thank Dr. Billy N. Day, of the Animal Husbandry Department, University of Missouri, who carefully read the text and made many valuable criticisms.

Examples used for illustrative purposes have been restricted to animals where it has been possible to do so. This has been done because such examples should be of more interest to students and breeders than those dealing with plants, and because the use of such examples afforded the opportunity to explain the inheritance of some very important traits.

It is hoped that the material presented here will not only be useful to the animal breeder who has been in business for a *number of years*, but will also be useful in training a new generation of animal breeders in whose hands lies the fate of the livestock industry in years to come.

CONTENTS

Glossary of Abbreviations

ix

1 Some Important Changes in Livestock Production

1

The development of the livestock industry in the United States Improvements have been made in the efficiency of livestock production Changes now taking place in livestock production The future of livestock production in the United States

2 Some Misconceptions about Genetics and Animal Breeding

7

Maternal impressions Inheritance of acquired characteristics Telegony Influence of age of the parents on the inheritance of the offspring

3 The Formation of Sex Cells—Carriers of Inheritance

13

The cell The chromosomes Formation of the sex cells Spermatogenesis Oogenesis Fertilization Relative importance of sire and dam

4 The Smallest Unit of Inheritance—the Gene

24

The gene How genes function When genes express themselves Genes vary in their expression Some cases of variations in gene expression

5 Types of Gene Action—Large Monofactorial Effects

35

Dominance and recessiveness with one pair of genes involved Incomplete dominance Multiple alleles Sex linked inheritance Sex influenced inheritance

- ✓6 Types of Gene Action—Two or More Pairs of Genes (44)
Polygenic inheritance Dihybrid inheritance Epistasis Over dominance Additive gene action
- 7 Linkage—Why Some Traits Are Inherited Together 52
Why some traits are inherited together How to test for linkage of genes Crossing over An example of linkage in poultry Practical significance of linkage in farm animals
- 8 The Laws of Probability and Animal Breeding 57
The concept of probability Probability and the segregation of genes in the gametes
- 9 Gene Frequencies in Populations 65
Gene frequencies The Hardy Weinberg Law What is a randomly mating population? Calculating gene frequencies in a population Some factors which modify gene frequencies

✓14	Principles of Selection	(123)
	<i>Natural selection. Artificial selection. Systems of selection for different kinds of gene action.</i>	
✓15	Selection of Superior Breeding Stock	(136)
	<i>Selection on the basis of individuality. Selection on the basis of pedigrees. Selection on the basis of collateral relatives. Selection on the basis of progeny tests. Methods of selection.</i>	
✓16	Some Factors Which Determine Selection Efficiency	(151)
	<i>Ability of the breeder to find superior breeding animals. Amount of selection pressure applied Heritability of the traits. Generation interval Genetic correlation among traits. Conclusions on progress in selection.</i>	
17	Principles of Inbreeding	159
	<i>Genetic effects of inbreeding. Consequences of homozygosity. Phenotypic effects of inbreeding. Physiological basis of inbreeding effects. Effect of inbreeding on different kinds of gene action. Possible uses of inbreeding. How to develop inbred lines.</i>	
18	How to Measure Inbreeding and Relationships	174
	<i>Preparing an arrow diagram of a pedigree. Calculating inbreeding coefficients. Coefficients of relationship. Direct relationships. Covariance tables for measuring inbreeding coefficients. Other methods of estimating homozygosity in a population.</i>	
19	Linebreeding	189
	<i>Illustration of linebreeding. Comparison between ordinary inbreeding and linebreeding. Why breeders favor linebreeding over inbreeding. Linebreeding in the past. When to linebreed.</i>	
20	Outbreeding and Crossbreeding	198
	<i>Genotypic and phenotypic effects of outbreeding and crossbreeding. Hybrid vigor or heterosis. How to estimate heterosis for economic traits. Genetic explanation of heterosis. What determines the degree of heterosis? Physiological basis of heterosis. Practical uses of crossbreeding. Practical use of outbreeding. Other systems of outbreeding.</i>	

21	Summary of Animal Breeding Principles	209
	<i>Sampling nature of inheritance Role of the animal breeder Information needed to formulate effective mating and selection systems When to use inbreeding and linebreeding When to use outbreeding and crossbreeding</i>	
22	Systems of Breeding and Selection in Swine	214
	<i>Traits of economic importance and how to measure them Heritability of economic traits in swine Selection indexes for swine Selection experiments with swine Selection for swine improvement in Denmark Genetic correlations between traits in swine Inbreeding results in swine Performance of crosses of inbred lines of swine Topcrossing Crossbreeding results with non inbred stock Conclusions regarding crossbreeding in swine Systems of crossbreeding Kinds of gene action affecting swine traits Programs for swine production New breeds of swine</i>	
23	Systems of Breeding and Selection in Beef Cattle	250
	<i>Traits of economic importance and how to measure them Correlation among performance traits in beef cattle Effect of inbreeding on performance traits in beef cattle Crossbreeding in beef cattle Kinds of gene action affecting economic traits in beef cattle Suggested program for purebred beef cattle production New breeds of beef cattle</i>	

GLOSSARY OF ABBREVIATIONS

ABA	<i>Animal Breeding Abstract</i>
AGSM	<i>Acta Genetica et Statistica Medica</i>
AJAR	<i>Australian Journal of Agricultural Research</i>
AJHG	<i>American Journal of Human Genetics</i>
AL	<i>Allatorvos; Lapok</i>
AN	<i>American Naturalist</i>
ArizAESR	<i>Arizona Agricultural Experiment Station Report</i>
BH	<i>The Blood Horse</i>
BMJ	<i>British Medical Journal</i>
BRNR	<i>Borden's Review of Nutrition Research</i>
C	<i>The Cattlemen</i>
ColoAESB	<i>Colorado Agricultural Experiment Station Bulletin</i>
DTW	<i>Deutsche Tierärztliche Wochenschrift</i>
FAOUN, LAAP	<i>Food and Agricultural Organization of the United Nations, European Association of Animal Production</i>
FlaAESB	<i>Florida Agricultural Experiment Station Bulletin</i>
FS	<i>Fertility and Sterility</i>
IowaAESRB	<i>Iowa Agricultural Experiment Station Research Bulletin</i>
ISGDR	<i>Illinois Swine Growers' Day Report, Urbana, Ill</i>
JAgS	<i>Journal of Agricultural Science</i>
JAR	<i>Journal of Agricultural Research</i>
JAS	<i>Journal of Animal Science</i>
JAUPR	<i>Journal of Agriculture of the University of Puerto Rico</i>
JDR	<i>Journal of Dairy Research</i>
JDS	<i>Journal of Dairy Science</i>
JEB	<i>Journal of Experimental Biology</i>
JEZ	<i>Journal of Experimental Zoology</i>
JG	<i>Journal of Genetics</i>
JGP	<i>Journal of Genetic Psychology</i>
JH	<i>Journal of Heredity</i>
JLCM	<i>Journal of Laboratory and Clinical Medicine</i>

MoAESRB	<i>Missouri Agricultural Experiment Station Research Bulletin</i>
NCRP	<i>National Council on Research Publication</i>
NHF	<i>National Hog Farmer</i>
N J AESB	<i>New Jersey Agricultural Experiment Station Bulletin</i>
NV	<i>Nordisk Veterinaermedicin</i>
NV-T	<i>Norsk Veterinaer Tidsskrift</i>
NZJST	<i>New Zealand Journal of Science and Technology</i>
NZJSTA	<i>New Zealand Journal of Scientific and Technological Agriculture</i>
PASAP	<i>Proceedings of the American Society of Animal Production</i>
PBRT	<i>Poultry Breeders' Round Table</i>
P6ICAH	<i>Proceedings of the 6th International Congress of Animal Husbandry</i>
P8ICG	<i>Proceedings of the 8th International Congress of Genetics</i>
PNAS	<i>Proceedings of the National Academy of Sciences</i>
PS	<i>Poultry Science</i>
PSB	<i>Proceedings of the Society of Biology</i>
PSCBC	<i>Proceedings of the Scottish Cattle Breeding Conference</i>
PSEBM	<i>Proceedings of the Society of Experimental Biology</i>

1

Some Important Changes in Livestock Production

MANY CHANGES IN LIVESTOCK PRODUCTION practices have occurred in the past and others will occur in the future. These changes are brought about by several different forces, some working together and some working separately. Two most important forces are changing consumer demands and the application of research results to improve the over-all efficiency of livestock production.

The successful livestock producer today and in the future must be a combination of livestock expert, business man, and prophet. He must use the best of approved practices and must use new research findings as soon as they become applicable. He must watch market fluctuations from month to month and from year to year, because the marketing of his animals at the right time is often as important as the cost of production in calculating profits. He must be a prophet in that he must anticipate and plan for future changes in demands for livestock and livestock products to be ready when they occur.

Experience gained from the past is often valuable in forecasting future events and trends. Therefore, it is important to discuss in a general way some changes in livestock production that have taken place in the past, those that are now taking place, and those that are likely to occur in the future.

THE DEVELOPMENT OF THE LIVESTOCK INDUSTRY IN THE UNITED STATES

When the first settlers came to America from Europe, they brought animals to supply meat, milk, and wool. These early animals were nondescript in appearance. Not until the work of Robert Bakewell and his contemporaries in England during the late 1700's do we find the

beginning of breeds and the use of the show ring and of records as a means of developing farm animals along special use lines. The work of these men led to the establishment of pure breeds of farm animals.

Purebred animals were first introduced into the United States after the Revolutionary War. The first purebreds to be imported were dairy cattle and sheep because milk and wool were two of the colonists' greatest needs. There were still enough wild animals in our woodlands and enough cull dairy cattle and sheep to supply meat. The need for more efficient meat-producing animals came later. Our present-day breeds of beef cattle and swine were imported shortly before the Civil War.

With the Industrial Revolution and the movement of people from farms into villages and cities, the need arose for more meat and wool to be used off the farm. This led to the realization that animals had to become more efficient in their production. The best method then known to increase the efficiency of production was to breed animals for purity of the desired characteristics. The use of this method contributed to the development of our pure breeds. The market for breeding animals was usually very close to home, and the breeders in a given area knew the breeding history of their neighbors' animals, so they knew where to get the types and breeds of animals they wanted for their herds or flocks. As the market for the sale of purebreds expanded and some breeders became better known than others, it became necessary to develop some means of verifying the ancestry of these animals. This led to the formation of breed associations during the last part of the 19th century.

The formation of breeds and their registry associations resulted in the recognition of the fact that purebred sires could bring about considerable improvement in livestock production. Numerous experiments were conducted by experiment stations prior to 1925 in which the offspring of purebred males were compared with those of nonpurebred males. In general, the comparisons favored purebred sires, and many livestock men became interested in the use of purebred or registered sires. Actually the word *registered* came to mean that the animal was something special.

With the formation of many breeds, the question inevitably arose of which was best. Many livestock men had their own ideas, and many of them made comparisons between different breeds, as did some of the colleges and experiment stations. These comparisons showed that there was no single best breed and that breeds differ in many performance traits. Breeds superior in some traits of economic importance were inferior in others. If this had not been found to be true, we would now have only one breed, or at most only a very few different breeds, in each of the classes of farm animals.

The increased popularity of the show ring in this country stimulated studies of several classes of farm animals to determine the best types from the standpoint of production. The general conclusion was that the correlation between type and performance was very low. This meant that

selecting for good type would not automatically give good performance. As far as the size of animals was concerned, however, an intermediate between large and small seemed to be the most desirable when all factors were considered.

Still later, interest was shown in crossbreeding both of cattle and of hogs, and many experiment stations compared crosses with purebreds. In general, the results favored the crosses, but in many cases the differences were small. These studies brought out the fact, however, that some breeds crossed better than others and that it was just as important in crossbreeding as in purebreeding to use good selection practices and a systematic mating system.

Recently, more and more emphasis has been placed on good records of performance of farm animals as a means of selection and improvement. Some new methods of testing, along with well-planned mating systems, show much promise in improving the efficiency of livestock production in the future.

IMPROVEMENTS HAVE BEEN MADE IN THE EFFICIENCY OF LIVESTOCK PRODUCTION

The application of improved methods of breeding, feeding, management, and disease control during the last few years has greatly increased the efficiency of livestock production. Estimates from agricultural statistics show that the production per animal unit in the United States has increased 30 per cent in the last 35 years. Efficiency of production has increased in almost all classes of livestock. Since dairy-cattle testing began in 1906, for all cows milked, the average milk yield per cow per year has increased 1700 pounds and the butterfat production has increased 63 pounds. About 30 years ago, well-fed hogs required 8 to 9 months to attain 200 pounds' weight and required 400 pounds of feed per 100 pounds of gain. During the past 10 years, the age to attain 200 pounds has been reduced to 5 to 5½ months, or even less, and only 300 to 325 pounds of feed are required per 100 pounds of gain. Ten litters at 6 months of age was the goal set up in some states 25 years ago. Today, litters weighing 2,000 to 3,000 pounds at that age are fairly common, and a few litters have weighed more than 5,000 pounds at 6 months.

Egg production per hen was increased about 81 per cent in the last 30 years. The production of broilers has increased greatly and has become an important industry in the United States; the efficiency of production also has increased. In 1917, 12½ weeks and 12.3 pounds of feed were required to produce a 3-pound broiler. In 1952, 10 weeks and 10.2 pounds of feed were required to produce a broiler of the same weight; more recently, even better results are being achieved on many specialized poultry farms.

CHANGES NOW TAKING PLACE IN LIVESTOCK PRODUCTION

The past century has seen a great change in farming and in the livestock industry in the United States. Farming has developed from small family operation to large scale, big business operation. Specialization is now the keynote. The old village general store of a few years ago has given way to the large, specialized stores of today. The farmer has turned from general farming operations, in many instances, to specialization in certain crops or livestock. Furthermore, he has become more specialized as to the type of livestock he produces, whether they are sheep, dairy cattle, beef cattle, swine, or poultry. Or, to paraphrase the old saying, farmers are tending to put more of their eggs in one basket."

Now that farming has become a big business, farmers are doing away with the small time system of mental bookkeeping. One cannot remember the milk production of an individual cow in the herd, even though some people think they can. Most likely to be remembered is that a particular cow produced a large pail of milk when she first freshened, but how quickly she slackened off in milk production is soon forgotten. The cow that gives an average amount of milk when she first freshens and maintains this level of production long into the lactation period is perhaps a better money maker than one whose production starts at a high level and declines rapidly.

The livestock industry in America is now facing increased competition for the home markets from substitute and synthetic products. For instance, oleomargarine has supplanted butter on most dinner tables of the working class. Lard is almost unheard of around the kitchen, with the increasing popularity of vegetable shortenings. Vegetable oils are not only an excellent product, but they can be produced more cheaply than animal fats. Nylon, orlon, and other synthetic fibers have put the silkworm out of business and are crowding the sheep from the forefront as a producer of clothing fibers.

To meet this competition, farmers will have to use greater care in the selection and breeding of their livestock. They will have to keep good records on each individual and carefully study these records to continue to make a profit in a livestock enterprise. Farmers can no longer cull only those animals that are noticeably below average in performance. In the future it will become increasingly necessary to cull substandard animals in order to meet competition.

THE FUTURE OF LIVESTOCK PRODUCTION IN THE UNITED STATES

The production of livestock should continue to be as important to the national economy in the future as it has been in the past, but there are

signs which point to the need for increased efficiency in the years to come. In addition, there are certain indications that the livestock producer will be forced to pay more attention to the quality of the product he offers for sale than he has in the past.

The population of the United States is increasing very rapidly. If it continues to increase at the present rate, it may some day become so large that there will be a problem of producing enough food. This might cause competition between humans and farm animals for the yearly production of cereal grains. The numbers of swine and poultry would then decline, since these would be the chief animal competitors. Even if this problem should develop, more efficient production of livestock through improved methods of breeding, feeding, and management would help to solve it. Cattle and sheep would offer less competition for the grain production, for there will always be millions of acres of land that can be utilized only for grazing purposes.

One other fact points to a greater need for efficiency in livestock production. Most of the tillable land in the United States is now in production, except some areas where irrigation could be practiced if water were available. Furthermore, thousands of acres of fertile farming land are being taken out of production by the growth of cities and towns and by the expansion and enlargement of "super" highways. Therefore, increases in the future food supply will have to be brought about by more efficient production and not by cultivating more new land.

Most farmers today are not thinking about increased production, but rather about the present farm crop surpluses. We should look to the future; we should not let temporary farm surpluses restrain progress in research. The development of new methods for the improvement of the efficiency of livestock production is a great challenge to research workers all over the world and should become increasingly important as time goes by.

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Questions and Problems

1. Why were purebred registry associations formed?

- 2 Trace the history of animal breeding research and practices from the time the first animals were imported from abroad to the present time
- 3 List several reasons why efficiency of production of livestock may become increasingly important in the future
- 4 If the United States should become overpopulated in the years to come what class or classes of livestock may be decreased in numbers? Why?

2

Some Misconceptions about Genetics and Animal Breeding

MODERN-DAY GENETICS HAD ITS BEGINNING in the year 1900, when the research paper by the Austrian monk, Gregor Mendel, on the inheritance of certain traits in plants was rediscovered. This report was first published in 1865, but received little attention at the time. Mendel carried out his experiments so carefully and interpreted the results so accurately that many of the principles and theories he described at that time still hold true today. Subsequent research has shown that his basic ideas were sound, although it is now known that a single trait may be affected by many genes and that genes interact in various ways in their expression.

Even after Mendel's discoveries, people still had many strange and false ideas about inheritance, some of which prevail to the present day. To the person who has not been trained in genetics they seem to have some foundation. For this reason, it seems advisable to discuss briefly some of these misconceptions.

In this chapter, we shall frequently refer to *mutations*. This term will be discussed in detail in Chapter X.

MATERNAL IMPRESSIONS

One false belief is that an unborn baby can be born defective if the mother is frightened by some object during pregnancy. An example of this occurred in the development of the Ancon breed of sheep. Shortly after the Revolutionary War, a New England farmer, Seth Wright,¹ noticed in his flock a ram lamb with very short and crooked legs. Because this lamb was short-legged and could not jump fences easily, Mr. Wright decided to start a new breed by mating this ram to the ewes in his flock. He named the breed "Otter" because, beside the fact that the sheep re-



FIGURE 1 THE PRESENCE OR ABSENCE OF HORNS IN CATTLE IS DETERMINED BY GENES WITH THE ABSENCE OF HORNS DOMINANT TO THE HORNED CONDITION (COURTESY OF THE AMERICAN HEREFORD ASSOCIATION)

seemed an otter in length of leg and body conformation, he thought that the mother of that first crooked and short legged lamb had been frightened by an otter during pregnancy. Modern day geneticists recognize that the occurrence of the strange ram lamb in Mr Wright's flock was due to a mutation or change in certain hereditary factors in the germ plasma of the lamb's ancestors and not to the frightening of its mother. The term *Ancon*, incidentally is derived from the Greek word meaning 'bent elbow'.

Even today some people still believe in maternal impressions. In a small community in south Missouri a few years ago a baby was born with a large mark on one cheek that resembled a patch of fur. Some local residents claimed that the mother had been frightened by a rat before the child was born.

INHERITANCE OF ACQUIRED CHARACTERS

Another misconception people have is that the offspring can inherit some change in the parent (or the ancestors over generations) acquired as an effect of the parent's environment. This can best be explained by citing examples.

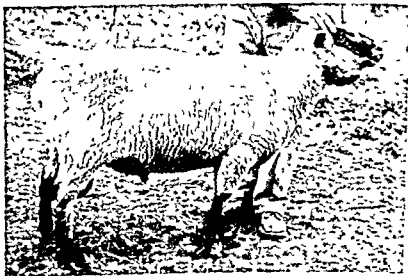
Most livestock producers know that some breeds of beef cattle are

horned and some are polled (have no horns). The polled character is desirable in the feed lot because the cattle fight less, need less trough space, and cause less injury. Some people have believed that the polled cattle originated because the horns were removed from breeding animals for many generations and this repeated removal finally caused the appearance of naturally polled calves.

How did polled cattle originate if acquired characters are not inherited? With our present knowledge of genetic principles, we know that the presence of horns, or their absence, in cattle is dependent on certain inherited factors which sometimes change from one generation to another. We also know that the rate of appearance of polled calves in a horned herd is about 1 in 20,000. Together, these factors indicate that the appearance of polled calves from horned parents is the result of a mutation or sudden change in the hereditary factors in the horned parents.

The origin of the polled breed of Hereford cattle is interesting. Warren Gammon and son of Iowa are credited with the breeding of the first polled Herefords.² These men communicated with hundreds of breeders of purebred horned Herefords all over the United States in a search for breeding stock that were naturally polled at birth. In other words, they searched for the polled animals in horned herds where mutations had occurred. They found and purchased seven polled cows and four polled bulls. These served as a foundation for the polled Hereford breed. The Gammons increased the numbers of polled cattle by proper mating and selection among the offspring of the polled parents. Some matings also were made in which polled cattle were mated to horned cattle; the polled calves from these matings were saved for breeding purposes. The fixing of pureness for polledness in the breed has been difficult, but it can be done and is now easily understood from a genetic standpoint. The genetic reasons for this will be explained in a later chapter.

FIGURE 2. A MATURE RAM WHICH WAS BORN WITH A SHORT TAIL. THIS WAS NOT DUE TO THE FACT THAT THE TAILS OF HIS ANCESTORS HAD BEEN DOCKED BUT BECAUSE SOME CHANGE OCCURRED IN THE GERM PLASM OF HIS ANCESTORS.



Most farm boys who have raised sheep know that it is desirable to dock lambs (cut off their tails) at an early age. One of the main reasons for doing this is to prevent screw worm infestations around the base of the tail in warm, moist weather. If the tails of lambs are not docked, manure and urine residues collect and often produce a moist condition near the base of the tail where screw worm eggs may be deposited and develop into the screw worm larvae. The larvae, after hatching, burrow into the flesh of the lamb and cause considerable damage or even death in some cases. The tails of lambs have been docked on most farms for many years throughout the United States. If acquired characters are inherited, we should have many breeds of sheep by now which are born with short tails. This, of course, is not the case.

A few years ago, lambs with short tails were born in a herd of sheep in central Missouri. An examination of the herd records indicated that the short tails were due to a mutation or change in the inherited factors of some of the lamb's ancestors. The inheritance of this trait does not seem to be simple, however, and it has not been possible to develop a breed of sheep all of which have naturally short tails. Some lambs sired by a short-tailed ram have short tails, some have tails of medium length, whereas others have tails of normal length. It appears that this trait in sheep will be much more difficult to fix in a breed than polledness was in cattle.

TELEGONY

This is the name for those instances in which a sire is supposed to influence all other offspring of the female to which he is mated even

FIGURE 3 THE SIRE AND DAM OF THESE GILTS HAD A WHITE BELT OF MEDIUM WIDTH, YET THESE GILTS SHOW A VARIATION IN BELT WIDTH FROM NONE, TO ONE WHICH IS VERY WIDE. THIS ILLUSTRATES VERY WELL THAT "LIKE DOES NOT BEGET LIKE."



when she is mated to other males. This is just a superstition and has no proof, yet there are many breeders today who still believe that it is true.

The idea of telegony probably originated in England many years ago, when an Arabian mare of a solid color was mated to a male Quagga. A Quagga is a zebra-like horse which has definite stripes around its body. The colt from this mating had stripes on its neck and withers and resembled the Quagga parent in this respect. Colts born to this same mare when she later was bred to an Arabian stallion also seemed to have faint stripes on their bodies. This led animal breeders to believe for a time that the first male parent to which a female was bred could influence her later offspring from other males. This idea has been disproved, however, and it is certain that telegony does not exist. It is interesting to note that the pure Arabian colts could have had faint stripes on their bodies, since it has been found that the Arabian breed of horses does carry stripes that are usually covered or hidden by the more solid color.

INFLUENCE OF AGE OF PARENTS ON THE INHERITANCE OF THE OFFSPRING

The age of the parents at the time of mating has no influence on the heredity of their offspring. This is true because each of the parents has throughout its life the same heredity composition with which it was born. One possible exception to this is the occurrence in the animal of gene mutations, and these may accumulate with age. Exposure to radiation, for example, can cause mutations. If these occur in the body cells, they have no effect on the offspring, for they cannot be transmitted. If the mutations occur in the germ cells, they can be transmitted to the offspring.

Each parent contributes equally to the inheritance of each of their offspring. Their contribution is made when the spermatozoon (male sex cell) and the ovum (female sex cell) unite to form the new individual. No additional inheritance is given to the offspring by either parent after that time. The mother has a great influence on her offspring during the early part of its life, but this influence is not of a hereditary nature. In farm animals, the mother carries and nourishes the young within her body from the time the young are conceived until they are born. In addition, she usually nourishes the young through the milk she produces until they are weaned. The mother, then, can influence the size and health of her young, depending on how well she feeds and cares for it during the period when it is entirely under her care. The only influence the male farm animal has on its young is through the inherited factors it transmits through the male sex cell.

From the standpoint of genetic make-up, then, as already mentioned, the age of the bull to which a young heifer is bred is not the cause of her

difficulty at calving time. The bull can influence the size of his calves at birth only through inheritance, as has been shown by several experiments. In general, a heifer produces larger calves and has more difficulty at calving time when bred to a bull with a large frame, regardless of his age, than when bred to one with a small frame.

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Questions and Problems

1. What is meant by maternal impressions? Does the mother influence her offspring in any way? Explain.
2. List some of the reasons why you think acquired characters are not inherited. What is responsible for the sudden occurrence of some trait in the offspring that has never been observed in the parents or in any of their ancestors?
3. Does the age of the male parent influence the size of the offspring at birth? Explain.
4. Does the age of the female parent influence the size of the offspring at birth? Explain.
5. Why do some parents have offspring that do not resemble them in some traits?

3

The Formation of Sex Cells— Carriers of Inheritance

MANY YEARS AGO SCIENTISTS THOUGHT that life could arise spontaneously from nonliving matter. But as man learned more about biology, he discovered that this was not true. Now scientists agree that all life must spring from pre-existing forms of life through the process of reproduction. Not a single case is known of verified spontaneous generation (development of living individuals from non-living matter).

Even the very youngest livestock producer is aware of the fact that cows, ewes, mares, and sows must mate with males of the species before they can produce young. Thus, they know that the new life in some way comes from both parents and that in many ways the young resemble their parents for recognizable traits.

Reproduction, or the development of a new individual, results from the union of an *egg*, or *ovum*, produced by the female parent and a *spermatozoön* produced by the male. These reproductive cells are so minute that they can only be seen clearly with a microscope. Each sex cell carries a sample one-half of the inheritance possessed by each parent.

Reproduction is such a delicate and complex process that one wonders that farm animals are so fertile. The physiology of reproduction is a complete and fascinating subject and many textbooks have been written on the subject. The purpose here is not to discuss the complex mechanisms involved in the physiology of reproduction, but rather to explain the nature of the hereditary material passed from the parents to their offspring and the mechanism involved which insures that each new offspring receives one-half of its inheritance from its sire and the other one-half from its dam.

THE CELL

The bodies of all animals are made up of microscopic "building blocks" called *cells*. The body contains many millions of cells of different sizes and shapes. They are all alike in that they contain two major parts, the cytoplasm and the nucleus. This is illustrated in Figure 4. The outer portion of the cell is the *cell membrane*, which serves as a framework and maintains the shape of the cell. By proper staining methods, cells can be seen to contain an oval shaped body more or less near the center called the *nucleus*. The nucleus might be said to be the heart and brain of the cell, and it is the part that is important in inheritance. The material between the nucleus and the cell membrane is called the *cytoplasm*. Within the cytoplasm are various bodies that play important parts in the function of the cell but, at least in farm animals, have little or nothing to do with the transmission of inheritance.

THE CHROMOSOMES

When the cell is properly prepared and stained, a number of thread like bodies appear within the nucleus. These microscopic threads are called *chromosomes*. One of the outstanding facts about the chromosomes is that they are present in pairs in the body cells. The members of each pair are very similar in appearance and might be called twins. Geneticists call these pairs *homologous chromosomes*, which is another way of saying that they are very much alike in appearance (*homo* comes from the Greek word meaning equal or the same, and *logus* from the word meaning proportion).

The different species of farm animals differ in the number of pairs of homologous chromosomes their cells possess. Chromosomes are very difficult to count, but it is generally agreed that swine possess 19 pairs, cattle and horses 30 pairs, and sheep 27 pairs. On the other hand, within a single species of farm animals the number of pairs of chromosomes is constant, e.g. swine have 19 pairs of homologous chromosomes regardless of the breed. The same is true of the other species of farm animals, all the different breeds possessing the number of pairs of chromosomes characteristic of that particular species.

Each pair of homologous chromosomes is distinct from the other pairs. It is important to remember that an individual receives one member of each pair of homologous chromosomes from its father and the other member from its mother. Each individual, in turn, will pass on to each of its offspring one member of each pair of chromosomes it possesses. Which one of the members of each pair the individual will receive from its par-

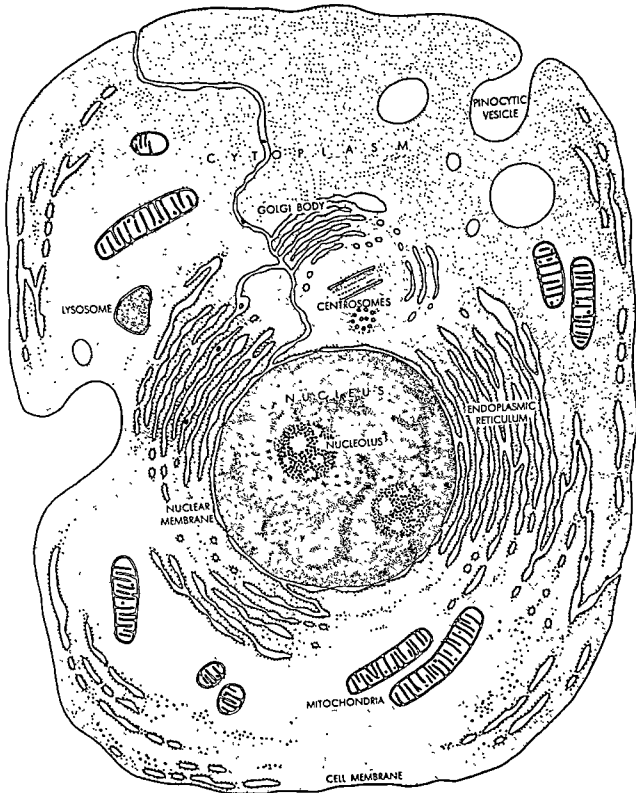


FIGURE 4. DIAGRAM OF A TYPICAL CELL BASED ON STUDIES MADE WITH THE ELECTRON MICROSCOPE. THIS SHOWS THAT THE CELL IS MUCH MORE COMPLEX THAN WAS THOUGHT SEVERAL YEARS AGO. (COURTESY OF THE *Scientific American*.)

ent is dependent upon chance, and there is no way of predicting which it will be. Another important fact to remember is that both members of a pair are not passed to the offspring, but only one of each pair.

There are some rare exceptions to this. Studies of human chromosomes show that certain abnormal individuals, mongoloids, possess more than the normal number of chromosomes for the species. Humans normally

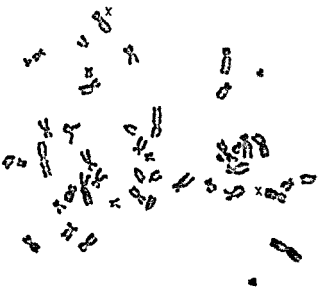


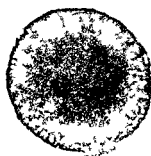
FIGURE 5 CHROMOSOMES OF THE HUMAN FEMALE (COURTESY OF TJIO AND PUCK, *Proceedings of the National Academy of Sciences*, 44 1229 1958)

possess 23 pairs of chromosomes but mongoloids possess an extra chromosome or a portion of one. It has also been found that an extra X (sex determining) chromosome is present in the body cells of individuals afflicted with a disease called Klinefelter's syndrome. Also it is theoretically possible for individuals to possess less than the normal number of chromosomes but this situation probably is lethal, for such individuals have not been observed.

FIGURE 6 ALL OF THE INHERITANCE THAT AN OFFSPRING RECEIVES FROM ITS PARENT COMES FROM THE OVA AND THE SPERM WHICH UNITE IN THE PROCESS OF FERTILIZATION. MILLIONS OF SPERM ARE EJACULATED AT ONE MATING FOR EACH EGG PRODUCED BY THE FEMALE (COURTESY OF THE UNIVERSITY OF MISSOURI)



BOAR SPERM
(1000 X)



SOW OVUM
(340 X)

FORMATION OF THE SEX CELLS

The breeding value of farm animals depends upon their ability to produce a large number of high-quality offspring. Basically, this ability depends on the production of normal, viable sex cells by both the male and female: *spermatozoa* by the male, and *ova* by the female.

The sex cells differ from body cells in that they contain only one member of each pair of homologous chromosomes (haploid number, $1n$) instead of both members (diploid number, $2n$). For instance, each body cell in the pig contains 19 pairs of homologous chromosomes, or a total of 38. Each sex cell contains one chromosome of each of these 19 pairs or a total of 19 chromosomes. The process of cell division that results in the formation of the sex cells and the halving of the chromosome number is known as *meiosis*. This reduction process is necessary in sex-cell formation in order to maintain a constant number of chromosomes from generation to generation. If reproductive cells carried the diploid rather than the haploid number of chromosomes, a doubling of the number of chromosomes would result in each new generation. Soon the chromosomes would become so numerous in each nucleus that cell division and growth of the body tissues could not occur in a normal manner.

SPERMATOGENESIS

Spermatogenesis is the process of spermatozoa formation which takes place in the testes of the normal, mature male. The male possesses two testicles, which are carried in the scrotum. Within each testicle are many small tubules, which can be seen by proper staining and preparation of the testicular tissue. These are called *seminiferous tubules* and in them the development of the spermatozoa takes place.

The process of spermatogenesis is shown diagrammatically in Figure 7. The original cells in the seminiferous tubules from which the spermatozoa develop are the primordial germ cells or *spermatogonia*. These are also often called "primitive" germ cells, which means that they are the original cells from which the spermatozoa develop. The primordial germ cells contain both members of every pair of homologous chromosomes. Thus, they contain all of the pairs of chromosomes for that particular species. For purposes of illustration, however, only three pairs of homologous chromosomes are shown in Figure 7.

The spermatogonium goes through regular cell division and forms two primary spermatocytes, each containing the diploid number of chromosomes. Proper staining methods show, however, that each member of a pair of chromosomes has doubled, so that, instead of two homologous

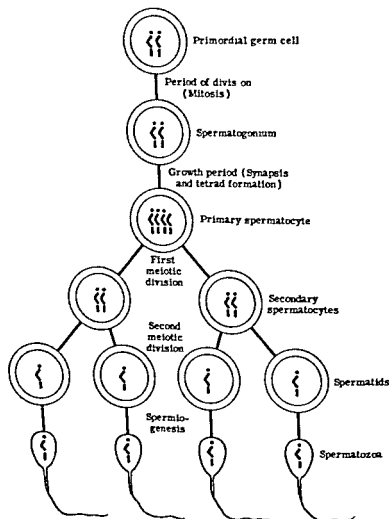


FIGURE 7 SCHEMATIC DIAGRAM OF SPERMATOGENESIS IN FARM ANIMALS (ONLY THREE PAIRS OF HOMOLOGOUS CHROMOSOMES ARE USED AS AN EXAMPLE.)

chromosomes there are four. This is the tetrad (from the Greek word meaning four) stage. These bodies now are called *chromatids*. In the next two cell divisions, each primary spermatocyte gives rise to two secondary spermatocytes and these give rise to a total of four spermatids. The four chromatids appearing in a primary spermatocyte are distributed equally throughout two divisions so that each secondary spermatocyte receives two chromatids and then each spermatid receives one, the chromatid then again becomes known as a chromosome.

We can consider the reduction through these meiotic divisions in this way: 1 primary spermatocyte (each $4n$) \rightarrow 2 secondary spermatocytes (each $2n$) \rightarrow 4 spermatids (each $1n$).

The spermatid represents the final division in the process of spermatozoa formation. During its development into a spermatozoon certain changes in form occur, which give the cell motility.

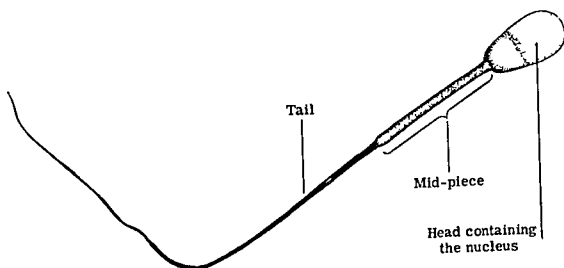


FIGURE 8 DRAWING OF A RAM SPERMATOZOON MADE FROM AN ACTUAL ENLARGED MICROPHOTO TO SHOW THE VARIOUS PARTS IN THEIR ACTUAL PROPORTION

The spermatozoa of the different species of farm animals are very similar in form and structure. Figure 8 shows a mature spermatozoon and its parts. The head of the sperm cell consists almost entirely of nuclear material and thus carries the chromosomes. The tail and midpiece are formed from the cytoplasm, and contain the motor mechanism which speeds the spermatozoon toward the egg at the proper time. In one sense, the sperm cell may be compared to a torpedo with a warhead, containing an explosive, and a propelling mechanism. The warhead of the sperm would be the head, containing the hereditary material, the tail and midpiece would be the propelling mechanism.

Spermatozoa are so small that a cubic centimeter would contain billions of them. It is startling sometimes to think how such a tiny cell could be of such vital importance from the standpoint of inheritance.

Normal, fertile, male farm animals produce from 800 million to 20,000 million spermatozoa per ejaculate. The numbers are influenced by many factors. Nevertheless, many millions of spermatozoa are delivered to the

TABLE 1
SEMEN PRODUCTION IN MATURE MALE FARM ANIMALS*

Class of Farm Animal	Semen Volume per Ejaculate in c. c.	No Sperm per mm ³ of Semen	No Sperm per Ejaculate	Life of Sperm in Female Tract
Boar	200	100,000	20 billion	24 to 40 hours
Stallion	100	60,000	6 billion	4 to 6 days
Bull	5	800,000	4 billion	28 to 30 hours
Ram	0.8	1,000,000	800 million	34 to 40 hours

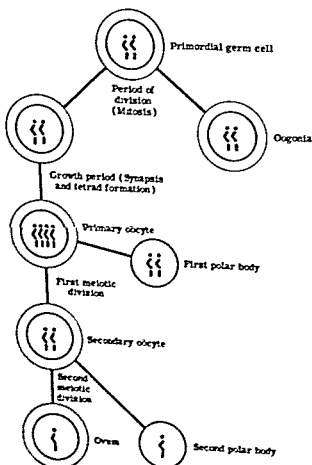
*Average and approximate figures

female reproductive tract during a single service. From 60 to 70 per cent of these cells are capable of uniting with the ovum to form a new individual, but only one is needed. The presence of great numbers of spermatozoa increases the chances that one will meet and unite with the ovum.

OÖGENESIS

The production of female reproductive cells occurs in the ovary, and the process is called *oögenesis*. Each ovum develops from a primordial or primitive germ cell, the *oögonium*. The steps involved in *oögenesis* are outlined in Figure 9. The process of *oögenesis* is similar to that of spermatogenesis with respect to meiosis, that is, the divisions effecting reduction

FIGURE 9 SCHEMATIC DIAGRAM OF OÖGENESIS IN FARM ANIMALS. (ONLY THREE PAIRS OF HOMOLOGOUS CHROMOSOMES ARE USED AS AN EXAMPLE.)



of chromosome number. The $4n$ condition appears in the primary oöcyte and the $1n$ condition in the ovum.

The way ovum production differs from sperm production is in the distribution of cytoplasm during meiosis. From Figure 9, it may be seen that only one functional ovum results from each primary oöcyte, whereas four functional spermatozoa result from each primary spermatocyte. From the division of the primary oöcyte, the products are one relatively large cell, the secondary oöcyte, which receives practically all the cytoplasm, and one much smaller cell, the first polar body, which receives practically no cytoplasm. (These two cells each have the $2n$ condition.) Again, in the division of the secondary oöcyte, one product, the ovum, receives practically all the cytoplasm, and the other, the second polar body, receives practically none. (The ovum and the second polar body each have the $1n$ condition.) The polar bodies are resorbed by the ovarian tissue, although it is possible that the first polar body ($2n$) goes on to complete meiosis to form two more cells (each $1n$). In either case, none of the polar bodies is functional in the remainder of the reproductive process.

The two main features of oögenesis, then, are the production of an ovum containing the $1n$ number of chromosomes and the development of a large amount of cytoplasm or yolk that is responsible, at least partially, for nourishing the newly formed individual until it makes contact with the uterus and blood supply of the mother through the placental membranes.

Female farm animals produce a limited number of ova at the time of mating. The mare and cow usually produce only one, whereas the ewe produces from one to three, or sometimes more, and the sow from 15 to 20. Ovulation, or the release of the ova from the ovary, usually occurs

TABLE 2

REPRODUCTION IN MATURE FEMALE FARM ANIMALS*

<i>Class of Farm Animal</i>	<i>Number of Days Between Estrous Periods</i>	<i>Length of Estrous Period</i>	<i>Time of Ovulation</i>	<i>Life of Ovum After Ovulation</i>
Sow	21	2 to 3 days	Second day of estrus	24 hours
Mare	21	5 to 6 days	24 to 48 hours before estrus ends	4 hours
Cow	19 to 20	16 to 20 hours	14 hours after end of estrus	20 hours
Ewe	16 to 17	24 to 30 hours	One hour before end of estrus	24 hours

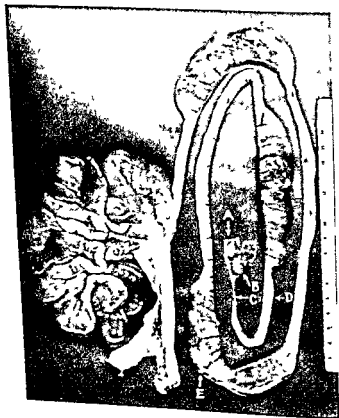
*These figures are averages and only approximate and are subject to considerable variation

while the female is in heat, although sometimes ovulation does not occur until after the end of the heat period. By this timing, mating occurs when the release of the ova and the introduction of the spermatozoa into the female reproductive tract coincide. Mating at the proper time is important, because the egg lives only a few hours after it is released from the ovary unless it unites with a spermatozoon. The life of the spermatozoa in the reproductive tract of the female is also limited to only a few hours.

FERTILIZATION

Fertilization is the process in which the sperm and egg unite to form a new individual. It occurs within the reproductive tract of the female within a few hours after the ovum is released from the ovary, usually in the upper part of the Fallopian tube.

From a genetic standpoint, the important feature of fertilization is that it restores the chromosome number of the new individual to that of the parents, so that once more the homologous chromosomes are paired. Thus, one member of each homologous pair is brought to the new individual by the spermatozoon and the other member by the egg.



RELATIVE IMPORTANCE OF SIRE AND DAM

The sire and dam contribute equally to the genetic make-up of each offspring. Genetically, then, for a single individual the sire and dam are of equal importance.

The sire is more important from the genetic standpoint, however, when the entire herd is taken into consideration. For example, consider a herd of 30 beef cows which are mated to a single bull and each produces a calf. In this case, the bull supplied one-half of the inheritance for all 30 of the calves, whereas each cow supplied only one-half of the inheritance for the one calf she produced. This is why the bull is the most important single individual in the breeding herd, and great care should be exercised in his selection. This does not mean, however, that cows are not important also, aside from the genetic aspect, because they nourish each calf from conception to the time it is weaned and can have a great influence on its growth and development throughout its life.

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Questions and Problems

1. Name the different parts of a cell.
2. Which is the most important part of the cell as far as the hereditary material is concerned? Why?
3. What is the major difference between the body cells and the sex cells?
4. List the main differences between the processes of spermatogenesis and oögenesis.
5. Which is the most important single individual in a herd? Explain.
6. What event occurs, important from the genetic standpoint, during the process of fertilization?

4

The Smallest Unit of Inheritance—the Gene

THE USE OF REFINED TECHNIQUES AND more effective equipment has yielded excellent results in recent years in the study of the gene and has added a great deal to the knowledge of the nature and function of the gene. Much more will be learned in the future. This phase of genetic research has reached the exciting stage, and much effort is being spent in more intensive studies on the nature of the gene.

A knowledge of the gene and of some of its functions is necessary to obtain a good foundation in the principles of animal breeding. This chapter will discuss some of the fundamental concepts of the gene and its action.

THE GENE

The gene is the smallest biological unit of inheritance, and it is carried on a chromosome. Hundreds and possibly thousands of genes are carried on each chromosome, each in a fixed or special position called a *locus*. The existence of a particular gene can be determined genetically only because it exists in at least two forms having different effects that can be observed readily in the organism. These forms are called *allelomorphs*, and they usually affect a trait in contrasting manners.

Genes are so small that they cannot even be seen with the ordinary type of microscope. Even if we could use a microscope powerful enough to enlarge the gene image to visible size, we could not be certain what to look for. Nevertheless, scientists have been able to learn quite a lot about the gene by using very special methods of study.

The chemical composition of the gene has been studied indirectly, by the chemical analysis of the chromosomes.² Chromosomes have also been

studied by special staining techniques, by their absorption of ultraviolet light, and by digestion experiments with the enzyme, deoxyribonuclease, and with proteolytic enzymes. These studies have shown that the chromosomes contain proteins and nucleic acids bound together in the form of nucleoproteins.

Two kinds of nucleic acids occur in cells.⁴ These are DNA, a short term for deoxyribonucleic acid, and RNA, or ribonucleic acid. Deoxyribonucleic acid is always found in the nucleus of the cell, and mostly in the chromosomes. Proof of this is the fact that twice as much DNA is found in the diploid body cells as is found in the haploid sex cells. RNA is found mainly in the cytoplasm. Chemically, these two nucleic acids are very similar. Each consists of a long chain of phosphate and sugar molecules with small side groups, called bases, attached to the sugars. DNA contains the sugar, deoxyribose, whereas RNA contains a slightly different sugar, ribose. Chemical studies and studies with viruses suggest that DNA is the primary genetic material, and that a gene is a segment of a DNA molecule. Electron microscope pictures show that the DNA molecule is long and rather stiff, like a piece of cord, and X-ray analysis shows that it is actually a double molecule or chain with one chain wrapped around the other in a helical structure. The bases connect two chains at various points.

Proteins are the basic material of life; they are formed in the cytoplasm. It is now thought that the genes send codes for protein structure to the cytoplasm by means of RNA. A mutated gene, inherited from a parent, sends a *wrong code*, and a genetic defect may occur. A study of such defects gives a clue as to how genes function normally.

HOW GENES FUNCTION

Gene action can be determined only if it affects some trait in the individual. Most of the knowledge of gene action has come through studies of genetic defects, resulting from mutations. In some cases, the mutations have been caused by exposure of the individuals to X-rays, but in most cases they have been caused by some, as yet unidentified, factors in the external or internal environment. These studies have shown that the function of genes is chemical in nature.

One of the first known cases of the genetic control of a specific chemical reaction was found in the rare metabolic disease in man called alcaptonuria.⁸ This disease is characterized by the hardening and blackening of the cartilage of the bones and the blackening of the urine when exposed to the air. The black urine is due to an accumulation of homogentisic acid. In the normal person, the enzyme is present that is responsible for the change of homogentisic acid to aceto-acetic acid, which is clear in the

urine. The person with alcaptonuria lacks this enzyme, so homogentisic acid accumulates in abnormal amounts in the urine.

Phenylketonuria in humans is another example of insufficiency of a particular enzyme. In this disease, phenylalanine hydroxylase, necessary for the normal metabolism of phenylalanine, is lacking. Abnormal metabolites accumulate in the tissues, and most affected individuals are idiots or imbeciles.

Albinism is a condition caused by an enzyme deficiency of genetic origin. Albinos lack the pigment, melanin, in the hair, skin, and eyes. Melanin is probably formed from tyrosine through the action of tyrosinase. When tyrosinase is not active, no pigment is formed in the individual, and it is an albino.

Another group of genetic defects in humans appears to involve the production of abnormal forms or the failure to produce a certain protein. Agammaglobulinemia seems to fit into this group, and has been described only recently.⁵ This term refers to the failure of production of gamma globulin in the body and its lack in the blood. A newborn baby receives

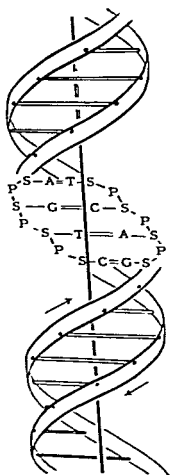
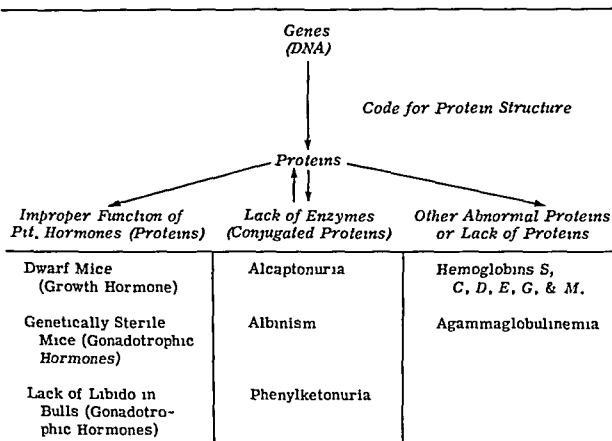


FIGURE 11 DIAGRAMMATIC REPRESENTATION OF THE WATSON-CRICK DNA STRUCTURE. P, PHOSPHATE; S, SUGAR. A, ADENINE; T, THYMINE; G, GUANINE; C, CYTOSINE. THE HORIZONTAL PARALLEL LINES SYMBOLIZE HYDROGEN BONDING BETWEEN COMPLEMENTARY BASES. (FROM MISSOURI AGRICULTURAL EXPERIMENT STATION RESEARCH BULLETIN 588)

TABLE 3

HOW GENES FUNCTION AS ILLUSTRATED BY SOME REPORTED
GENETIC ABNORMALITIES IN HUMANS AND ANIMALS



Note Many other examples are known that could be added to this list, but these show how genes act.

a supply of gamma globulins from its mother before birth, but this supply gradually decreases to near zero at four months of age. Normally, the baby's own gamma globulin production begins at about three weeks of age and reaches a high level by five to eight months. The lack of gamma globulins results in increased susceptibility to bacterial infections because of the lack of resistance from antibodies in the blood.

A second example of genes in man that appear to function in the control of the production of a particular protein is that revealed by the gene defect causing sickle-cell anemia.¹² In the individual having this disease, the red blood cells have the shape of a sickle instead of the normal round shape. This disease is confined largely to populations in central Africa, southern India, and a region of Greece, or descendants of these peoples. In normal humans, only hemoglobin A is found in the red blood cells. The sickle-cell gene apparently results in the production of an abnormal form of hemoglobin called hemoglobin S.

Individuals of genotype (actual genetic makeup) $H_A H_A$ produce hemoglobin A and no hemoglobin S. Those of genotype $H_A H_S$ produce both

hemoglobin *A* and hemoglobin *S* and both are detectable in the blood with neither gene affecting the expression of the other. Individuals of this genetic makeup seldom have anemia and when they do it is slight. When the cells are deprived of oxygen however they may assume the sickle rather than the normal shape. This genetic makeup is usually referred to as the sickle-cell trait. Individuals of genotype H_AH_S produce mostly hemoglobin *S* and usually die of anemia. Studies of the hemoglobin in the blood of normal and affected individuals show that the two hemoglobins differ slightly in their electrical charge and can be separated by electrophoresis and paper chromatography.

Individuals of the H_AH_S genetic make up seldom live to reproduce, unless given frequent blood transfusions and special medical care. Thus there is a strong natural selection against the H_S gene. However, in certain tribes in Africa it has been found that as high as forty per cent of the individuals in the tribe were of genotype H_AH_S or showed the sickle cell trait. This was very difficult to understand since H_AH_S individuals seldom if ever, lived to reproduce. Later work¹ showed that the H_AH_S individuals were more resistant to malaria than the normal H_AH_A individuals and thus natural selection favored the H_AH_S individuals whereas both those which were normal or had sickle-cell anemia died at a more rapid rate.

More recently, sickle-cell anemia has been used as a very important means of studying the mode of action of genes.⁷ By a very detailed separation and chemical analysis of the amino acids in the hemoglobin of normal and sickle-cell individuals it was found that the two hemoglobins contained the same types of amino acids but differed in the amounts of one of the polypeptides. The peptide from the normal persons contained two glutamic acid units and one valine whereas the abnormal peptide contained one glutamic acid unit and two valines. Thus valine replaced one glutamic acid unit in the abnormal hemoglobin. The importance of this study was that a mutation caused an abnormal protein to be produced. This gives added support to the theory that a gene carries the code which controls the construction of the protein molecule for which it is responsible.

Evidence is also accumulating that hormone production by the pituitary gland or the action of these hormones may be under genetic control. If true this would fit in very well with the theory that mutations result in the production of defective proteins. Hormones from the anterior pituitary are protein in nature.

Dwarfism in mice has been shown to be a genetic effect¹⁰ resulting in a lack of growth hormone secreted by the anterior pituitary gland which stimulates body growth.

Sterility in an obese strain of mice has been reported to be due to a genetic defect.¹² The ovaries of the females seem to have normal repro-

ductive capacity but remain immature, either because of an inadequate release of gonadotrophic hormones from the pituitary or the inactivation of the hormones after their release. Ovulation, implantation, gestation, parturition, and lactation have been induced in these mice after a series of treatments with the various hormones. An inherited defect in bulls causing lack of libido (sex drive) has been attributed to the failure of the anterior pituitary gland to secrete adequate amounts of a particular hormone or to the inactivation of the hormone.⁹

Further study of such inherited defects should be quite helpful in determining how genes function in growth and reproduction in all species, including farm animals, and could lead to improved methods of more efficient and economical livestock production.

WHEN GENES EXPRESS THEMSELVES

Many people are of the opinion that traits determined by genes are always present or visible at birth. This is not true, because the time at which genes express themselves is variable. In sheep, an inherited condition has been found in which the lambs are born with short tails. The genes for this trait express themselves early in embryonic life when the bones were being formed. Genes for eye color in humans usually begin to show their effects a few weeks after birth, and not at birth. A form of muscular dystrophy in humans is not expressed until the age of seven to fifteen years. Hereditary baldness affects most individuals only after maturity, at 25 to 30 years of age. The gene for Huntington's Chorea, a nervous disorder in humans, may not affect the individual until he is past 50 years of age.

The fact that genes do not always express themselves early in life may also be important in animal breeding. It is probably unwise to make a practice of selecting breeding stock at the time of birth. It is more advisable to make selections at market age, for by that time the genes will have expressed themselves in a favorable or unfavorable manner.



FIGURE 12 VARIATION IN THE EXPRESSION OF GENES FOR
TAIL LENGTH IN SHEEP

Penetrance of a gene is the frequency of its actual expression of a trait as compared with the frequency at which it is expected to be expressed. The degree of penetrance of a gene is usually referred to in terms of percentages and can vary from almost zero to 100 per cent. A gene which expresses itself only 30 per cent of the time is said to possess 30 per cent penetrance.

Genes may vary in both penetrance and expressivity. Little is known of the importance of this in selection for more efficient production of livestock except that environment can mask or change the way genes express themselves. Often environmental effects are mistaken for gene effects and selection for traits so influenced is not effective. This will be discussed in more detail in a later chapter.

SOME CAUSES OF VARIATIONS IN GENE EXPRESSION

Many factors may be responsible for variations in gene expression. In general, variations may be divided into two groups: those due to external environmental conditions and those due to internal environment.

EXTERNAL FACTORS

Temperature can play a very important part in the expression of genes. One of the best known examples of this effect in animals is in the Himalayan breed of rabbits.² The gene responsible for coat pattern causes the production of an enzyme which is necessary for the formation of a black pigment. However, only the extremities of the body, such as the nose, ears, feet, and tail, are pigmented, whereas the main parts of the body are white. The explanation of this difference is that the enzyme does not form at normal body temperatures but does form at slightly lower temperatures; hence, pigment appears in the body extremities where the

temperature is presumably lower. A similar explanation has been made for the coat pattern in the Siamese cat.

Studies of bread mold, or *Neurospora*, give a clue as to the possible explanation of the temperature sensitivity of the pigment-forming system in Himalayan rabbits and Siamese cats.² Melanin is formed in this organism, and in one strain the pigment formation shows a strong temperature effect. Cell-free tyrosine-containing preparations of a strain of *Neurospora* in which temperature does not affect pigment formation and a similar preparation of the temperature-sensitive strain show quite clearly that their differences in response to temperature are due to different temperature stabilities of their tyrosinases. The tyrosinase of the temperature-sensitive strain is much less stable *in vitro* at 35°C.

Sunlight is also known to affect the ability of genes to express themselves. One example is found in certain Southdown sheep where hypersensitivity to sunlight is a heritable trait.⁶ In affected lambs, the liver does not function properly, and there is a failure to excrete phyloerythrin, an end-product of chlorophyll digestion. This product accumulates in the blood stream and in certain areas of the skin, where it is activated by sunlight. Eczema develops over the face and ears, and the animals may even die if left outdoors; but if they are kept indoors and allowed to graze at night, they do not develop symptoms. Cancer eye in Hereford cattle is also thought to be inherited,³ and many ranchers believe that the condition is aggravated in regions of intense sunlight, such as the southwestern portion of the United States.

FIGURE 13. CANCER EYE IN CATTLE. THIS CONDITION IS QUITE PREVALENT IN ANIMALS IN THE SOUTHWESTERN UNITED STATES. IT IS HERITABLE AND SEEMS TO BE INCREASED IN INCIDENCE IN AREAS OF INTENSE SUNLIGHT. (COURTESY OF THE UNIVERSITY OF TEXAS, M.D. ANDERSON HOSPITAL & TUMOR INSTITUTE.)



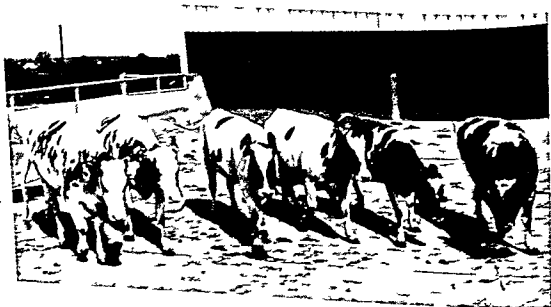
INTERNAL FACTORS

Of the various internal environmental factors which may affect genes expression the hormones are probably among the most important. Earlier we pointed out that a gene for dwarfism in mice apparently has its influence through the failure of the production of the growth hormone by the anterior pituitary gland. Other genes for growth are present but cannot express themselves because of the lack of this hormone.

In humans there is considerable evidence that the tendency to contract diabetes is inherited but this tendency often is not manifested unless the pancreas is overloaded by the individual's consumption of large amounts of carbohydrates over a long period of time.

The sex hormones are also known to influence gene expression. Baldness in humans is often hereditary but is expressed more often in the male. The same is true of the mahogany and white color in Ayrshire cattle. Boars are known to possess from 25 to 35 inches less back fat at market weight than barrows from the same litters on the same kind of feed. Bull calves on the average almost always outweigh heifer calves at weaning time and the difference seems to widen as the calves grow older. Dairy bulls carry genes for milk production and roosters carry genes for egg production but neither of these traits is expressed in the males of the species.

FIGURE 14 SPOTTING IN SOME BREEDS OF CATTLE IS DUE TO A SINGLE PAIR OF RECESSIVE GENES BUT MODIFYING GENES CAUSE A VARIATION IN SPOTS FROM INDIVIDUALS WHICH ARE ALMOST WHITE TO THOSE WHICH ARE ALMOST BLACK. THESE THREE SETS OF IDENTICAL TWINS SHOW THE UNIFORMITY OF SPOTTING WITHIN TWIN SETS BUT GREAT VARIATION BETWEEN DIFFERENT SETS. (COURTESY OF MOORMAN MANUFACTURING COMPANY QUINCY ILLINOIS)



Genes on one pair of chromosomes may modify the expression of another pair of genes on a different pair of chromosomes. These are called modifying genes. Spotting of the coat in Holsteins is due to a single pair of genes. Yet, coats vary from almost white to almost black, and have black spots of various sizes. Selection in either direction for size of spots is successful, indicating that other genes (modifying genes) are responsible for the expression of the genes for spotting. The possibility of the existence of other modifying genes in farm animals could be important from the standpoint of avoiding errors in selective breeding for important traits.

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12. SMITHBERG, M., and M. N. RUNNER. "Pregnancy Induced in Genetically Sterile Mice," *JH*, 48:97, 1957.

Questions and Problems

1. What is a gene and what are some of its most important properties?

- 2 Give several examples of inherited defects which illustrate how genes function
- 3 What evidence do we have that genes do not always express themselves at the time of birth? How could this be of importance to the animal breeder?
- 4 What are some of the causes of variations in gene expression?
- 5 Why is it of importance in animal breeding to know why genes vary in their expression?

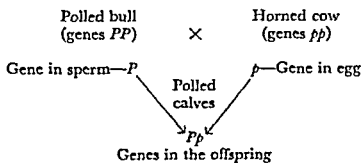
5

Types of Gene Action—Large ✓ Monofactorial Effects

IN THE PREVIOUS CHAPTER, IT WAS pointed out that each chromosome carries hundreds and possibly even thousands of different genes. Some of these genes affect only one trait, whereas others affect several. Also, the same trait may be affected by many different pairs of genes. A thorough knowledge of the different types of gene action is important in order to understand and use genetics to devise satisfactory mating and selection systems for the improvement of farm animals.

DOMINANCE AND RECESSIVENESS WITH ONE PAIR OF GENES INVOLVED

Now let us see just how genes work together to bring about the expression of given characters. Take, for example, the condition of horns in cattle. The symbol P will be used to designate the gene for absence of horns and p to represent the gene for presence of horns. If a pure polled bull (PP) is mated to a group of horned cows (pp), what kinds of calves will be produced? The calves receive one-half of their genes from the bull and one-half from the cow. It can be seen from the following diagram, which shows a single mating, that the calves will receive the P gene from the sire and the p gene from the dam, for the sire carries only genes for polledness, and the dam carries only genes for horns.



The polled gene (P) is said to be *dominant*. Therefore, the calves will all be polled even though they also carry the gene for horns. The ability of the polled gene to block out or cover the expression of the horned gene is called *dominance*. The gene for horns, then, is said to be *recessive* to the polled gene, because it takes a back seat, so to speak, in its presence. When two genes affecting a character in different manners occur together in an individual, and occupy identical locations on each member of a pair of homologous chromosomes, this individual is said to be *heterozygous* (in this, the calves, Pp). For this reason, all of the calves from the mating of a pure polled bull to pure horned cows will be heterozygous, that is, each will carry one gene for horns and one for polled. These two genes in the heterozygous animal are called *alleles* (allelomorphs) of one another, because they both affect the same characteristic in the individual but in different manners. When the two genes affect the character in the same manner, as is the case in the horned cows (pp) and the polled bull (PP), the animal is said to be *homozygous*. This genetic construction is called the *genotype*. The expression of the genotype is called the *phenotype*.

What would the offspring be like if two of these heterozygous polled (Pp) individuals were mated? If we remember that genes occur in pairs in the animal's body cells and that one or the other of these genes of each pair is present in the sperm or egg, we can see that each of these polled individuals, which are heterozygous, can produce two kinds of sex cells. One sperm or egg will carry the gene P and the other the gene p . By a diagram that combines the genes from the eggs and the sperm in all possible ways, it can be seen that one half of the offspring have the same genotype as that of the parents, one fourth have the same genotype as that of the polled grandparent, and the other one fourth have the same genotype as that of the horned grandparent.

Polled bull (genes Pp)	×	Polled cow (genes Pp)
Genes in sperm P or p		Genes in egg P or p

Possible combinations of sperm and eggs

- 1 PP Pure for polled (homozygous)
- 2 Pp Polled (heterozygous)
- 1 pp Pure for horns (homozygous)

It will be observed that three genotypes appear, in a definite ratio 1 PP 2 Pp 1 pp . This, then, is called a *genotypic ratio*. Two of the genotypes give rise to the same phenotype, however. And the distribution of phenotypes in the offspring is called the *phenotypic ratio*. All the calves carrying Pp and PP are polled, while only the one carrying pp has horns. From the above diagram, it can be seen that the phenotypic ratio in the offspring of this mating would be 3 polled 1 horned.

The PP and the pp individuals are said to breed true, or to be pure, since they are homozygous and can pass only one kind of gene to their offspring. The Pp individuals, however, never breed true, that is they do not have 100 per cent Pp offspring, because they are heterozygous and pass two kinds of genes through their sex cells to their offspring.

From the foregoing discussion, we can state some facts that must be remembered clearly for a better understanding of the inheritance of a trait where only one pair of genes is involved. These are (1) genes occur in pairs in the body cells of the individual, (2) one of each pair came from the father and one from the mother, (3) the genes of a pair separate during formation of sex cells, and (4) on fertilization, the genes are re stored to the paired condition.

The law of chance determines which sperm and which egg will combine at the time of fertilization to form the new individual. The 1 2 1 genotypic ratio for the offspring of two heterozygous (Pp) individuals works well on paper, but under practical conditions the actual ratio may be far from the expected. Actually, when a small number of offspring are produced from such a mating, all might be of one genotype of either PP , Pp , or pp . The larger the number of offspring produced, however, the more likely it is that the expected ratio will occur. A similar condition is observed in the number of boys and girls that may occur in any one family. The chances of any one baby being a boy is one out of two, for it has an equal chance of being a boy or girl. Yet, many of us have seen even large families where all the children are of the same sex. This happens because of the law of chance. This will be discussed more fully in the chapter on probabilities.

Six different kinds of matings, with reference to parental genotype, are possible when one pair of genes is involved and where dominance is complete. These are listed in Table 4, together with other comments about such matings.

INCOMPLETE DOMINANCE

Occasionally, we find modifications of this simple two gene inheritance, as for example, the case of coat color in Shorthorn cattle. Three different coat colors appear in the Shorthorn breed—red (RR), roan (RW), and

TABLE 4

VARIOUS KINDS OF MATINGS WHICH CAN BE MADE AND THE RESULTS OF SUCH MATINGS WHERE ONE PAIR OF GENES AFFECT A GIVEN TRAIT AND DOMINANCE IS COMPLETE

Genotype of Parents	Genotypic Ratio of Offspring	Breeding Ability of Offspring*
$PP \times Pp$	$\begin{cases} 1 PP \\ 1 Pp \end{cases}$	Breeds true Doesn't breed true
$PP \times PP$	All PP	All breed true
$PP \times pp$	All Pp	None breed true
$Pp \times Pp$	$\begin{cases} 1 PP \\ 2 Pp \\ 1 pp \end{cases}$	Breeds true None breed true Breeds true
$Pp \times pp$	$\begin{cases} 1 Pp \\ 1 pp \end{cases}$	None breed true All breed true
$pp \times pp$	All pp	All breed true

*The term *breeds true* means that individuals of this genotype transmit only one kind of gene to their offspring. Heterozygous genotypes don't breed true because they may transmit either of two genes to their offspring.

white (IVW). When a roan bull (RIW) is mated to a group of roan cows (RIW) the offspring will be colored in the ratio of one red (RR) to two roan (RIW) to one white (IVW). It should be noted that this is the same genotypic ratio that is obtained when dominance is complete, and as in the example where polled was dominant to horned. But in this instance the heterozygote expresses itself phenotypically in a different manner from either homozygote and the genotypic and phenotypic ratios are the same 1 2 1. This type of gene action is called *incomplete dominance*, or a blending type of inheritance. One practical point here is that, even though it is not possible to develop a pure breeding roan herd (RIW), because the roan individuals are all heterozygous and will not breed true, it is always possible to produce roan cattle (RIW) by mating a red parent (RR) to a white parent (IVW).

Many cases of inheritance are known where dominance is incomplete and the genotypic and phenotypic ratios of the offspring of a mating between heterozygous parents are the same. For example palomino horses will not breed true because they are heterozygous for genes for color, but they can always be produced by mating chestnut sorrels with pseudo albinos.¹ Another example is in Compress Herefords which are heterozy



FIGURE 15. A COMPREST HEREFORD BULL ON THE LEFT AND A CONVENTIONAL HEREFORD BULL ON THE RIGHT. (COURTESY H. H. STONAKER, COLORADO STATE UNIVERSITY.)

gous for the comprest gene. When mated, comprests produce offspring in the ratio of 1 normal (cc) to two comprest (Cc) to one dwarf (CC). Of course, in this instance it is impossible to mate the normals (cc) with the dwarfs (CC) to produce all comprest (Cc), because the mortality rate of the comprest dwarfs is so high that they do not survive to maturity and cannot be used for breeding purposes.

An important fact concerning selection when dominance is incomplete is that the genotype can be determined by inspection of the phenotype. Therefore, an undesirable gene can be eliminated from the herd by discarding all heterozygotes.

MULTIPLE ALLELES

Previously we defined alleles as those genes which occupied the identical loci on homologous chromosomes but affected the same trait in a different manner. Research work in genetics and animal breeding has demonstrated that in a population there may be more than two alternative genes that can occupy the loci. Such genes are called *multiple alleles*.

The best-known series of multiple alleles is that which affects blood types in humans. Three different genes are known to be involved, and these are called genes A , B , and O . These three genes may be combined to form several genotypes, as follows: individuals belonging to blood group A may be of the genotype Aa or AA ; those of blood group B , of genotype Ba or BB ; those of blood group O of genotype aa , and of blood group AB , of genotype AB . Only two of the three alleles occur in any one individual, since there are only two locations on homologous chromosomes that are available for these genes.

A large series of multiple alleles and several blood groups are known to exist in farm animals,² and a knowledge of these may be used to identify the parents of offspring in particular instances.

SEX LINKED INHERITANCE

Farm animals are known to possess from 19 to 30 pairs of chromosomes in the body cells depending on the particular species involved. Each pair of homologous chromosomes segregates independently of the other pairs when the sex cells are formed. One pair of homologous chromosomes is called the *sex chromosomes*. One of the pair is called the *X* and the other the *Y* chromosome. All other pairs of chromosomes are referred to as *autosomes*.

The female possesses two *X* chromosomes in the body cells, and the male possesses an *X* and a *Y* chromosome. Many different genes are carried on each of the sex chromosomes as is true of the autosomes.

The following example illustrates how the *X* and *Y* chromosomes transmitted by the parents to the offspring.

Female	Male
<i>XX</i>	<i>XY</i>
Kind of sex chromosome in the sex cells	
Eggs (<i>X</i> only)	Sperm (<i>X</i> and <i>Y</i>)
Sex of offspring	
<i>XX</i> or Female	
<i>XY</i> or Male	

Thus the male offspring receives its *Y* chromosome from the father and its *X* chromosome from the mother and the female receives one *X*-chromosome from the mother and one from the father.

When we speak of sex linked traits we refer to those traits determined by genes carried (linked) on the *X* chromosome. Very little is known about the importance of sex linkage in farm animals probably because it has not been studied as much in animals as it has in humans. Undoubtedly future studies in genetics will reveal several sex linked traits in farm animals.

The *Y* chromosome is shorter than the *X* chromosome and so cannot carry all the genes corresponding to those on the *X* chromosome. Therefore in the male it is possible for a single recessive gene on the extra portion of the *X* chromosome to express itself. In the female there must be two recessive genes on the *X* chromosomes just as on autosomes for a recessive trait to be expressed.

A further difference between sex chromosomes and autosomes is that a portion of the *Y* chromosome is not homologous to the *X* chromosome and in a few instances known in humans a gene is carried on the *Y*-chromosome and is responsible for the appearance of a trait in the male. This is referred to as *holandric inheritance*. An example in humans is webbed

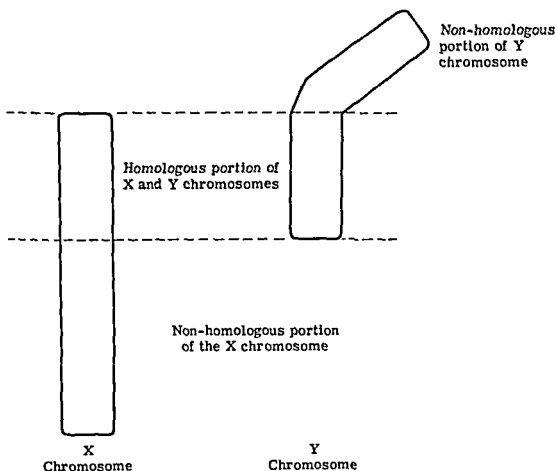


FIGURE 16. A DRAWING WHICH ILLUSTRATES THAT SOME PARTS OF THE X AND Y CHROMOSOMES ARE NOT HOMOLOGOUS. THUS, ONLY ONE RECESSIVE GENE ON THE NONHOMOLOGOUS PORTION OF EITHER SEX CHROMOSOME IS ALL THAT IS NEEDED FOR THE GENE TO EXPRESS ITSELF.

toes, and it is passed from father to son for generation after generation. In general, however, sex-linked traits are determined by genes carried on the X-chromosomes.

Agammaglobulinemia in humans, mentioned in Chapter 4, is a sex-linked recessive trait, and the gene for it is carried on the X-chromosome. Let us use the letter *A* for the normal gene and the letter *a* for the gene which causes agammaglobulinemia. Let us also assume, for an example, that a woman who is a carrier of this gene (genotype $X_A X_a$) marries a man who is not affected by this disease ($X_A Y$). The following diagram gives the genotypes of the boys and girls one would expect, with respect to this trait:

Carrier woman		Normal man
$X_A X_a$	×	$X_A Y$
Genotypes expected in offspring:		
1 $X_A X_A$		Normal girl
1 $X_A X_a$		Carrier girl
1 $X_A Y$		Normal boy
1 $X_a Y$		Boy with agammaglobulinemia

Daughters from such a marriage would have equal chances of being carriers of the defective gene, but none would contract the disease. The sons, on the other hand, would have equal chances of receiving a normal or a defective gene from their mother, and since only one gene carried on the X chromosome is necessary for the expression of this trait in the male, those receiving the gene for agammaglobulinemia from the mother would be afflicted by this disease.

The importance of sex linked genes for type and performance in farm animals is not definitely known. But they are probably not very significant, for type and performance in animals are influenced by many pairs of genes most of which are carried on the autosomes.

SEX INFLUENCED INHERITANCE

This type of inheritance is often confused with the sex linked type. The genes for sex influenced inheritance are carried on the autosomes, and their expression is influenced by the sex of the individual. In the heterozygote, the genes usually are expressed as dominant in the male and as recessive in the female. The inheritance of horns in sheep is a good example of a sex influenced trait. Table 5 gives the genotypes and phenotypes for this trait.

Since the sex of the individual or more probably the male hormone production, can cause a definite difference in the expression of genes for horns in sheep it is interesting to speculate how the same kind of situation could exist for other traits in farm animals. For instance, it is known that boars possess from 25 to 35 inches less backfat than litter mate barrows but there is considerable variation among litters. Possibly a boar could have very thin backfat at market weight because of a high level of male hormone production. This condition might not be transmitted to his castrate male offspring because their male hormone production would practically cease at the time of castration. Another way of stating this problem is to ask whether we actually know what characteristics we would look for in the intact breeding males in order to select those that will produce the most desirable castrate male offspring.

TABLE 5

INHERITANCE OF HORNS IN SHEEP—A SEX-INFLUENCED TRAIT

Genotype	Phenotype of Rams	Phenotype of Ewes
HH	Horned	Horned
Hh	Horned	Hornless
hh	Hornless	Hornless

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- 1 CASTLE, W. E. "The ABC of Color Inheritance in Horses," *C*, 35 122, 1948
- 2 RENDEL, J. "Blood Groups of Farm Animals," *ABA*, 25 223, 1957

Questions and Problems

- 1 Define the following terms: dominant gene, heterozygote, homozygote, allelomorphs, phenotype, genotype, phenotypic ratio, genotypic ratio, sex-linked trait, sex-influenced trait, and multiple alleles.
- 2 The black color in Angus cattle is dominant to red. A black bull is mated to a black cow, and a red calf is produced. What are the genotypes of the two parents?
- 3 A swine breeder mates a boar to a half-sister, and a total of 36 pigs is produced in three litters. Eleven of these pigs are found to possess red eyes, whereas the remaining 25 pigs have eyes of normal color. Both parents also possess eyes of normal color. Is the gene responsible for red eyes dominant or recessive? Explain. What are the probable genotypes of the parents?
- 4 Starting with animals in Question 3, how would you develop a strain of hogs all of which would have red eyes?
- 5 In Hereford cattle, the compest gene (*C*) is incompletely dominant to the gene (*c*) for normal size, and the compest individuals are of the genotype (*Cc*). Outline a breeding program which you would recommend to develop a purebred strain of compest cattle. How would you eliminate the compest gene from the breeding herd?
- 6 A Shorthorn breeder has a herd in which some of the cows are white, some are red, and some are roan. His herd sire is roan in color. Outline a method in which he can develop a pure strain of red Shorthorns, starting with the above foundation animals.
- 7 Under practical conditions, which trait can be made homozygous more easily, one which is due to a dominant gene or one which is due to a recessive gene? Explain.
- 8 Red-green color blindness in humans is due to a sex-linked recessive gene. By an example, show how two parents of normal vision could have a color-blind son.
- 9 What would be the genotypes of the parents of a color-blind girl?
- 10 Many traits in humans are known to be due to a sex-linked recessive gene. Why have so many sex-linked traits been reported in humans? Why have so few been reported in farm animals?
- 11 List the main differences between sex-linked and sex-influenced inheritance.

6

Types of Gene Action—Two or ✓ More Pairs of Genes

POLYGENIC INHERITANCE

MOST TRAITS IN LIVESTOCK OF THE greatest economic importance, such as rate of gain, efficiency of gain, milk production, and carcass quality, are affected by many pairs of genes. Such inheritance is called *polygenic* inheritance. Polygenes may have very small individual effects, but, their over all action may be very great. Polygenes act together in such a way that their effects on a particular trait are additive or cumulative or complementary, to give what breeders refer to as a "nicking effect." These different actions of polygenes require that special selection and mating procedures be used to make the greatest possible progress in livestock production.

be $PPBB$, and that of the cows $ppbb$. The genotypes and phenotypes of the different generations may be illustrated as follows:

Generation

P_1 black Polled bull $PPBB$ \times red Horned cows $ppbb$

F_1 $PpBb$
All black Polled (mated *inter se*)

		Eggs			
		PB	Pb	pB	pb
F_2 Sperm	PB	$PPBB$ Polled black	$PPBb$ Polled black	$PpBB$ Polled black	$PpBb$ Polled black
		$PPBb$ Polled black	$PPbb$ Polled red	$PpBb$ Polled black	$Ppbb$ Polled red
	pB	$PpBB$ Polled black	$PpBb$ Polled black	$ppBB$ Horned black	$ppBb$ Horned black
		$PpBb$ Polled black	$Ppbb$ Polled red	$ppBb$ Horned black	$ppbb$ Horned red
	pB	$PpBB$ Polled black	$PpBb$ Polled black	$ppBB$ Horned black	$ppBb$ Horned black
		$PpBb$ Polled black	$Ppbb$ Polled red	$ppBb$ Horned black	$ppbb$ Horned red
	pb	$PpBB$ Polled black	$PpBb$ Polled black	$ppBB$ Horned black	$ppBb$ Horned black
		$PpBb$ Polled black	$Ppbb$ Polled red	$ppBb$ Horned black	$ppbb$ Horned red

Some new genetic terms are introduced in this example. The P_1 generation is that of the parents. The F_1 is the first filial generation, or the first generation of a given mating. The F_2 generation is produced by crossing the F_1 individuals. The term *inter se* means the mating of the F_1 generation among themselves.

All the sperm of the bull of genotype $PPBB$ contain one P and one B gene. All the eggs of the cows of genotype $ppbb$ contain only p and b genes. When the sperm and egg cells unite in fertilization, the genotype of all F_1 individuals is $PpBb$. Their phenotype is polled and black.

Individuals of the F_1 generation have the genotype $PpBb$ whether they are male or female, and they produce four different kinds of sex cells, PB , Pb , pB , and pb , in approximately equal numbers. Thus, any egg produced by the cows has an equal chance of carrying one of these four combinations of genes, and each of the eggs has an equal chance of being fertilized by a sperm of one of the four different kinds. From the checker-board, we see that among the 16 F_2 individuals there are 9 different genotypes and 4 different phenotypes. The phenotypic ratio of the F_2 generation is 9 polled black to 3 polled red to 3 horned black to 1 horned red.

An interesting point of such a cross is that the traits which were possessed by the grandparents have now been combined in different combinations in the F_2 generation, that is, the grandchildren. This illustrates

one of the laws of Mendel known as the Law of Independent Assortment of Characters and means that in this case genes affecting horns and coat color were inherited independently and therefore were on different pairs of homologous chromosomes

The principle of independent assortment of characters is often used in livestock breeding. For example, the Santa Gertrudis breed of cattle was developed from a cross of the Brahman and the Shorthorn breeds. In the formation of this new breed, selections were made to combine the heat and disease resistance of the Brahman with the beefiness of the Short horns. The principle has also been used in many other livestock breeding programs.

EPISTASIS

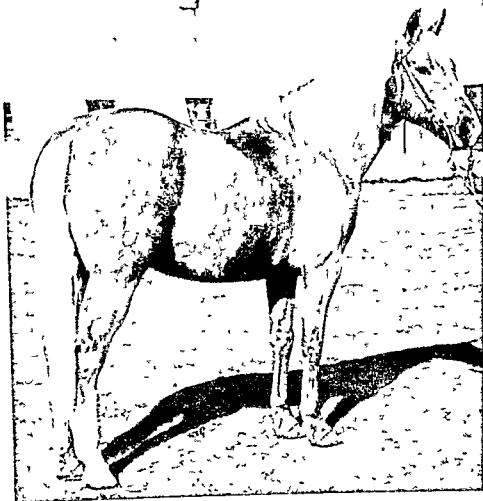
Epistasis is another type of variation in gene expression that may be of importance in livestock breeding. Epistasis is the name given to non linear interactions (where the effect of one gene does not add to the effect of another to influence the phenotype) of various kinds between any nonallelic genes. These may be interactions between genes on the same or on different chromosomes. In contrast, dominance is the nonlinear interaction between genes which are alleles.

Epistasis may be illustrated by coat color in horses.² The genetic bases of all the colors have not been established definitely, but they will serve to illustrate the point. In most animals there is a color gene *C* which is necessary for the expression of color. When it appears in the homozygous recessive form *cc* the coat color is white, a condition called albinism. Another gene that affects coat color is also found in some animals. This is the gene *D* for the dilution of color, and its effects are manifest in the palomino color in horses.

When a chestnut stallion (*AAbbCCdd*) is mated to a Type A albino mare (*AAbbCCDD*), a palomino colt (*AAbbCCDd*) is produced.² When two palominos are mated, it is possible to get colts of which one half are palomino, one fourth chestnut, and one fourth Type A albino. This is illustrated as follows:

P_1	Chestnut stallion <i>AAbbCCdd</i>	×	Type A albino mare <i>AAbbCCDD</i>
F_1	Palomino colts (mated <i>inter se</i>) <i>AAbbCCDd</i>		
F_2	1 <i>AAbbCCdd</i>	Chestnut	
	2 <i>AAbbCCDd</i>	Palomino	
	1 <i>AAbbCCDD</i>	Type A albino	

FIGURE 17. GRAND CHAMPION PALOMINO MARE AT A SHOW IN 1952 (COURTESY OF THE PALOMINO HORSE BREEDERS OF AMERICA.)



In this instance, the gene D is the controlling factor in coat color expression. When present in the homozygous recessive state (dd), color is present in the full amount (chestnut). In the palomino there is a dilution of color, and in the homozygous dominant state (DD), there is an absence of color, and the animal is white.

Many examples of epistatic gene action are known in mammals, and the genes act or interact in many different ways. In the preceding example, the gene D was dominant, or at least partially dominant, to its own allele, so this is referred to as dominant epistasis. Instances of recessive epistasis are known in which the epistatic gene is recessive to its own allele and has to be present in the homozygous recessive state in order to have its effect. One form of albinism in rats is due to recessive epistasis. Still other instances are known in which genes that are not alleles complement each other to produce an effect which neither pair of genes produces alone.

It is possible that epistasis has an important influence on the expression of genes that affect many of the economic traits in farm animals. Since these probably would deal with fundamental types of gene action, they might be difficult to identify. In spite of this difficulty, however, we can devise breeding and selection procedures to make the greatest use of these types of gene expression.

OVERDOMINANCE

Overdominance is another kind of gene action which may be of importance in animal breeding. It has been proposed as a theory, but in the past few years some examples have been found which give support to the proposal.

Overdominance is the interaction between genes that are alleles and results in the heterozygous individual being superior to either of the homozygotes. For example, three different genotypes such as A^1A^1 , A^1A^2 , and A^2A^2 may be used. According to this theory, alleles A^1 and A^2 together produce a reaction that they do not produce separately.

The principle of overdominance may be illustrated by the inheritance of a particular blood type in rabbits.³ Two alleles seem to be involved. One allele is responsible for the production of one antigen, and the other is responsible for the production of a second, different antigen. The heterozygous individual produces still a third separate antigen not found in either homozygote. Thus the two alleles interact to cause the production of an antigen which they do not cause in the homozygous state. A similar condition seems to exist in human haptoglobins¹ which are proteins with the specific property of binding hemoglobins. It has been proposed that two autosomal genes are involved. One homozygous individual causes the production of one haptoglobin, the other homozygote causes the production of a second, and the heterozygous individual causes the production of these two haptoglobins plus a third not found in either of the two homozygous individuals.

Overdominance probably involves many pairs of genes all affecting the same trait. The effect of any one pair of genes, however, could be rather small, but the combined effect of many pairs could result in a considerable advantage to the heterozygote. This kind of gene action, together with epistasis and dominance, could be responsible for the expression of hybrid vigor when certain lines, strains, or breeds are crossed.

ADDITIVE GENE ACTION

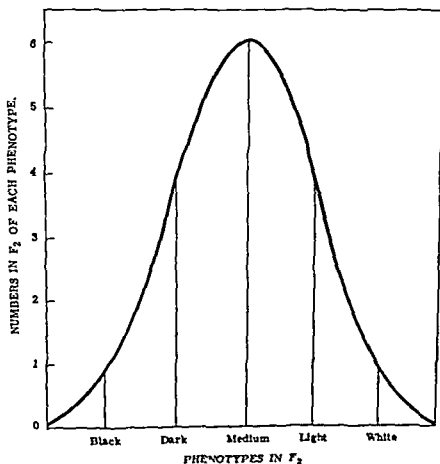
This is still another kind of polygene action in animals. In this type of inheritance, there is no sharp distinction between genotypes, but many gradations between the two extremes. Davenport's theory of skin-color inheritance in humans is a good example of additive gene action. Two different pairs of genes are thought to affect the production of pigment in the skin, although this may be an over-simplification of the actual mode of inheritance. In general, however, the theory seems to fit the mode of inheritance fairly well, although there are probably other genes involved.

The following example illustrates the principle of additive gene action:

P_1	Black skin $AABB$	×	White skin $aabb$
F_1	Medium (mulatto) (<i>inter se</i>) $AaBb$		
F_2	1 $AABB$	Black	
	2 $AABb$	Dark	
	1 $AAbb$	Medium	
	2 $AaBB$	Dark	
	4 $AaBb$	Medium	
	2 $Aabb$	Light	
	1 $aaBB$	Medium	
	2 $aaBb$	Light	
	1 $aabb$	White	

Five different phenotypes are observed, with a continuous gradation between white and black and no sharp distinction between any two classes.

FIGURE 18. ILLUSTRATION OF HOW THE DIFFERENT PHENOTYPES IN THE F_2 OF A MATING OF F_1 MEDIUM INDIVIDUALS (MULATTOES) ASSUME A FREQUENCY DISTRIBUTION CURVE.



The proportion of offspring of different skin colors in the F_2 generation would be

- 1 black,
- 4 dark,
- 6 medium (mulatto),
- 4 light,
- 1 white

These are shown in the form of a frequency-distribution curve in Figure 18 and it may be observed that a normal bell-shaped curve is formed

Genes *A* and *B* are called contributing genes because they make a contribution to the darkening of the skin. Genes *a* and *b* are called neutral genes because they contribute nothing or at least very little to skin color. An individual of the genetic composition of *aabb* is said to be of the residual genotype the genotype expressing the phenotype when no contributing genes are present.

An important aspect of additive gene action is that none of the genes is dominant or recessive. Each contributing gene adds something that makes the skin darker in color and the effects of each gene accumulate. Hence, the term additive gene action.

Additive gene action is thought to affect most traits in farm animals that are of economic importance although it has a much greater influence on some traits than on others. Growth rate, milk production, conformation, carcass quality as well as other traits are affected by this type of inheritance.

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3. COHEN, C. Occurrence of Three Red Blood Cell Antigens in Rabbits as the Result of the Interaction of Two Genes. S 122 35 1956

Questions and Problems

- 4 What is the difference between ordinary dominance and dominant epistasis?
- 5 Explain the differences between overdominance and epistasis
- 6 Solid color (S) in cattle is dominant to white spotting (s), and (L_w), which causes spotted animals to have less white, is dominant to its allele (l_w), which allows spotted animals to have increased amounts of white. A bull of solid color whose mother was white spotted with a large amount of white was mated to a cow which was white spotted but mostly white. If the offspring produced were white spotted but with little white, what was the genotype of the bull?
- 7 Assume you have a herd of black grade cattle which are polled. You mate them to a grade bull which is also black polled. In the first calf crop, some red calves are dropped, and some of the black calves as well as some of the red calves possess horns. If polledness is dominant to horns and black is dominant to red, what is the possible genotype of each of the parents of the red horned calves?
- 8 Using animals in question 7, outline a breeding and selection program you would follow to develop a pure breeding red polled strain of cattle.
- 9 If animals in question 7 were used which would be the simplest to develop, a pure strain of red horned cattle or one that was pure black polled? Explain.

7

Linkage—Why Some Traits Are Inherited Together

MENDEL'S LAW OF THE INDEPENDENT

Assortment of Characters does not always hold true, and Mendel was the first to notice this many years ago. The exception to this law has been observed in several species of plants and animals. Here we shall explain why this sometimes occurs and show how it might be of importance in livestock breeding.

WHY SOME TRAITS ARE INHERITED TOGETHER

Linkage is the presence on the same chromosomes of two genes affecting two traits. Instead of segregating and recombining in a random manner in subsequent generations, the genes travel together in the process of oogenesis and spermatogenesis and thus are inherited together.

It has been pointed out earlier that each chromosome carries hundreds of genes affecting different traits. The different traits determined by genes on the same chromosome tend to be inherited as a single group, and this is called a *linkage group*. The number of linkage groups corresponds to the number of pairs of chromosomes in a particular species. Not much is known about traits belonging to a single linkage group in farm animals, but our knowledge in this field should increase as research continues.

in the offspring, in approximately equal numbers. If the genes are linked, only two phenotypes will appear, and in approximately equal numbers.

To illustrate this method, let us use characters that are not linked and thus are inherited independently: polledness (P), which is dominant to horns (p), and black (B), which is dominant to red (b). When an individual of genotype $PPBB$ is crossed with one of genotype $ppbb$, all of the F_1 offspring will be of genotype $PpBb$ and of phenotype polled and black. When these F_1 individuals of the $PpBb$ genotype are backcrossed (or mated) to the homozygous recessive $ppbb$, the offspring produced will be:

4 $PpBb$ —polled, black
 4 $Ppbb$ —polled, red
 4 $ppBb$ —horned, black
 4 $ppbb$ —horned, red

Thus, the four different phenotypes will occur in approximately equal numbers, showing that the two pairs of genes are on two different pairs of homologous chromosomes.

Now, to show what would happen if these genes were linked, let us assume that P and B are together on one member of a pair of chromosomes and p and b are together on the other member. If linkage were complete and close, we would expect the following results from crosses:

P_1	Polled black $PPBB$	\times	Horned red $ppbb$
F_1	Polled black $PpBb$		
F_2	1 $PPBB$	Polled black	
	2 $PpBb$	Polled black	
	1 $ppbb$	Horned red	

In other words, polledness and black coat color would be inherited together, as would horns and red coat color. No horned black or polled red individuals would be observed in offspring as is the case when there is an independent assortment of the characters.

CROSSING-OVER

However, in almost all instances where linkage is involved and the test cross is made, all four phenotypes do occur in the next generation, but two appear more often than the other two. For instance, suppose that a back cross were made by mating F_1 individuals in the preceding example

to the homozygous recessive genotype, and the phenotypes were the following

45 $PpBb$ —polled, black
 5 $Ppbb$ —polled, red
 45 $ppbb$ —horned, red
 5 $ppBb$ —horned, black

This is not a 1 1 1 1 ratio expected in independent assortment, and we would have to conclude that linkage must be involved. But, during meiosis in the heterozygote, an 'accident' has occurred to the members of a chromosome pair in some of the sex cells. When they came together in the intimate process of synapsis,* they broke at about the same points, and exchanged parts. The result is that on some chromosomes P and b are together and on some p and B are together. This phenomenon is called *crossing over*. In the hypothetical example, the percentage of crossing-over is 10 (phenotypes where crossing-over occurred) divided by 100 (total number of phenotypes), times 100, or 10 per cent.

AN EXAMPLE OF LINKAGE IN POULTRY

Linkage of comb shape and leg length in chickens has been reported.³ Rose comb (R) is dominant to single comb (r) and the creeper (C) is dominant to normal leg length (c). Creeper chickens have very short legs that cause them to take very short steps so that they appear to creep when they walk. Individuals homozygous for the creeper gene die early in life, and thus this gene is a semilethal gene. When the test cross was made between a male heterozygous for both rose comb and creeper legs and females homozygous for both single comb and normal legs, the progeny produced were as follows:

Rose comb creeper $RrCc$	×	Single comb normal $rrcc$
Offspring		
22 $RrCc$		Rose comb, creepers
1 $Rrcc$		Rose comb, normal
33 $rrcc$		Single comb, normal
4 $rrCc$		Single comb, creepers

Thus the genes for rose comb and creeper legs were carried on one member of a chromosome pair, and the genes for single comb and normal legs on the other member. Some crossing-over occurred, however, as

* During the reduction division in spermatogenesis and oogenesis the chromosomes of a pair come together and twine around each other. This is the meaning of the term synapsis.

shown by the appearance of some rose comb normal and some single comb creepers in the progeny. The amount of crossing-over was about eight per cent.

In the double heterozygous offspring, where R and C remained together on one member of the chromosome pair, and r and c remained together on the other, the linkage is called *coupling*; where crossing-over occurred and genes R and c became linked, and r and C became linked, the disruption of linkage is called *repulsion*.

Genes located further apart on the same chromosome cross over more often than those that are closer together. In fact, the further apart they are the more difficult it becomes to distinguish crossing-over from the independent assortment of characters; thus, some linkages remain undetected. For this reason, there may be more instances of linkage in the traits of farm animals than we have been able to discover.

The degree of crossing-over has been used to determine approximately the loci of certain genes in some species. Maps of chromosomes have been made, showing approximate locations. Mapping has progressed quite rapidly for the fruit fly (*Drosophila*) and to a lesser extent for mice and humans. Very little chromosome mapping has been done for the various species of farm animals.

PRACTICAL SIGNIFICANCE OF LINKAGE IN FARM ANIMALS

Very little is known about the linkage of genes in farm animals. Detailed and extensive studies have been made of the blood groups in cattle, where it has been found that 10, and possibly 12, different pairs of the 30 pairs of chromosomes carry genes for blood groups. These genes must be linked with genes that determine other characters. The possibility of detecting such linkage associations depends on how closely the genes are linked and how frequently the linked genes are manifested.² If the linkage between blood group genes and genes for some other trait is strong, the blood group genes might be useful as chromosome markers. It seems doubtful that attempts to discover linkage associations between blood group genes and genes affecting economic traits would be very fruitful. The main reason for this is that so many different genes are involved and the expression of any single pair is weak. In addition, linkage associations would have to be determined for each animal, for linkage relationships would vary between individuals.

Furthermore, it is often difficult to distinguish between the effects of two closely linked genes and the pleiotrophic* effects of the same gene. A good example of this is found in chickens, where there is a series of alleles affecting blood group antigens at the B locus on the chromosomes. By

* Pleiotrophic effects means that the same gene may affect more than one trait.

test crosses, it has been found that hens homozygous for a certain *B* allele such as *BB* or *B'B'* produced eggs with decreased hatchability as compared to those heterozygous for *BB'*. Viability to nine weeks of age was also slightly greater in the heterozygous offspring!

In other instances in farm animals, there does seem to be a strong correlation between certain quantitative traits, such as rate of gain and efficiency of gain, but it is not assured that this correlation is due to linkage. These two traits are strongly associated probably because the genes affecting them do so through a common physiological pathway. Linkage could be involved, but is less likely, because of crossing-over and consequent equilibrium, which is dependent upon gene frequency and not on the degree of linkage.

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- 2 RENDEL, J. "Blood Groups of Farm Animals" *ABA*, 25 223, 1957
- 3 SEREBROUSKY, A. S., and S. G. PETROV. "A Case of Close Autosomal Linkage in the Fowl" *JH*, 19 305, 1928

8

The Laws of Probability and Animal Breeding

PRACTICALLY NOTHING OF GREAT IMPORTANCE in this life is known with absolute certainty. In spite of this, however, we have learned that we can predict more closely the outcome of an event by taking a calculated risk, that is, making a decision on the basis of what is most likely to occur. Even though we may not realize it, the concept of probability² is used for handling situations where our knowledge of the outcome is not exact. As far as animal breeding is concerned, the segregation of genes and their recombination in the union of the sperm and the egg at fertilization follow certain laws of probability.

THE CONCEPT OF PROBABILITY

The concept of probability is more easily illustrated than defined. We shall use P to represent the probability that an event will occur and Q to represent the probability that it will not occur. $P + Q = 1$, so that P is equal to $1 - Q$ and Q is equal to $1 - P$. Thus, if an event is certain to happen, the probability of its happening is equal to one. If it is certain not to happen, the probability of its happening is equal to zero. In all other cases between these two extremes, P ranges from zero to one.

Several rules may be applied to the combining of separate probabilities, but in animal breeding two of these are of the greatest importance. One rule states that the probability of occurrence of a single event that is one of a set of mutually exclusive events is the sum of the probabilities of the single events. The term, "mutually exclusive," means that the occurrence of one event in a given trial excludes the possibility of the occurrence of another event. For example, there are four aces and four kings in a deck of cards. If we pick one card from a deck, the probability of its being an ace is $\frac{1}{4}$, and the probability of its being a king is also $\frac{1}{4}$. Suppose

we are asked to determine the probability of picking either an ace or a king from a deck of cards. If we pick one the other is excluded, so we are dealing with mutually exclusive events. The probability of drawing either an ace or a king from a deck of cards is the sum of the two separate probabilities or $\frac{1}{13} + \frac{1}{13}$, or $\frac{2}{13}$.

The second rule states that the probability of two or more of a series of independent events occurring together is the product of the probabilities of occurrence of the single events. This rule applies to two or more events that occur independently of each other. In other words the occurrence of one does not exclude the occurrence of the other. For example, if we flip two pennies into the air, the probability that one will come up heads is not dependent upon which way the other lands. Likewise, if a parent is heterozygous for a pair of genes such as Aa , the probability that any one gamete will carry A is independent of the probability that any other gamete from that same parent will carry A (or a).

To illustrate the use of this rule let us determine the probability that two pennies tossed into the air will come up heads. The probability of the first penny coming up heads is $\frac{1}{2}$ the probability for the second penny is also $\frac{1}{2}$. The probability that both will come up heads is $\frac{1}{2}$ times $\frac{1}{2}$ or $\frac{1}{4}$. Similarly the probability of 4 pennies coming up heads if tossed together is $\frac{1}{2}$ times $\frac{1}{2}$ times $\frac{1}{2}$ times $\frac{1}{2}$ or $\frac{1}{16}$.

PROBABILITY AND THE SEGREGATION OF GENES IN THE GAMETES

To illustrate how the laws of probability apply to the segregation of genes in the gametes let us use two polled bulls of genotypes PP and Pp as examples. The probability that the bull of genotype PP will produce a sperm carrying the P gene is one the probability he will produce a sperm carrying the horned gene (p) is zero. The situation with the bull of genotype Pp is different however. The probability he will produce a sperm carrying the polled gene (P) is $\frac{1}{2}$ and the probability he will produce a sperm carrying the horned gene (p) is also $\frac{1}{2}$. The reason for this is the segregation of members of pairs of genes in the sperm.

Let us now apply the law of probabilities for two independent events to the gametes using two different traits in cattle horns and coat color. Black (B) coat color is dominant to red (b) and polled (P) is dominant to horns (p). The genes for color are carried on one pair of homologous chromosomes and the genes for horn conditions are carried on another pair. First let us use as an example a bull that is pure for both polled and black color ($PPBB$). If we consider each pair of genes separately we see that the probability of a sperm from this bull carrying P is one and the probability of its carrying p is zero. The probability of that same

sperm carrying *B* is also one and for its carrying *b* is also zero. What is the probability that such a bull will produce a sperm carrying both *P* and *B*? The answer is one, because the probability of both of these genes occurring together in the same sperm (two independent events) is the product of the two independent probabilities, which is 1 times 1, or 1. The probability of a sperm from such a bull carrying both *p* and *b* genes, of course, is 0 times 0, or 0.

Probabilities of the various combinations of *P*, *p*, *B*, *b* occurring in the sperm of a bull that is heterozygous (*PpBb*) is handled similarly and would be:

Gene	Probability of a sperm carrying this gene:
<i>P</i>	$\frac{1}{2}$
<i>p</i>	$\frac{1}{2}$
<i>B</i>	$\frac{1}{2}$
<i>b</i>	$\frac{1}{2}$

The probability of various combinations of the two different pairs of alleles occurring together would be:

Possible combinations of genes in the sperm	Probability of a sperm carrying these two genes
<i>PB</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>Pb</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>pB</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>pb</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$

PROBABILITY AND THE RECOMBINATION OF GENES IN THE ZYGOTES

The concept of probability and the combining of probabilities can now be expanded to the union of genes in the zygote (Fertilized egg). The examples used, of course, assume that the different pairs of alleles assort and recombine independently. First, let us use one pair of alleles for polled and horned cattle. The probability that gametes from parents of the three genotypes would carry one of each allele would be:

	Genotype of Parent:		
	<i>PP</i>	<i>pp</i>	<i>Pp</i>
Probability of <i>P</i> in a gamete	1	0	$\frac{1}{2}$
Probability of <i>p</i> in a gamete	0	1	$\frac{1}{2}$

Now we can calculate the probability of various combination of gametes occurring in the offspring of parents that are both heterozygous (*Pp*).

Genotype of offspring	Probability of this genotype
<i>PP</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>Pp</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>pP</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$
<i>pp</i>	$\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$

This corresponds to the 1:2:1 genotypic ratio in the offspring of crosses of heterozygous individuals, as we saw in Chapter 5

The following example illustrates the probability of various combinations of genes in the gametes when two separate pairs of genes are involved and the parents are heterozygous for both pairs of genes:

	Genotypes of:	
	Sire <i>PpBb</i>	Dam <i>PpBb</i>
Probability of <i>PP</i> in a gamete	$\frac{1}{4}$	$\frac{1}{4}$
Probability of <i>Pp</i> in a gamete	$\frac{2}{4}$	$\frac{2}{4}$
Probability of <i>pp</i> in a gamete	$\frac{1}{4}$	$\frac{1}{4}$
Probability of <i>BB</i> in a gamete	$\frac{1}{4}$	$\frac{1}{4}$
Probability of <i>Bb</i> in a gamete	$\frac{2}{4}$	$\frac{2}{4}$
Probability of <i>bb</i> in a gamete	$\frac{1}{4}$	$\frac{1}{4}$

The probabilities of different combinations of the genes in the offspring h parents would be:

<i>PPBB</i>	$\frac{1}{4} \times \frac{1}{4}$ or $\frac{1}{16}$
<i>PPBb</i>	$\frac{1}{4} \times \frac{2}{4}$ or $\frac{2}{16}$
<i>PPbb</i>	$\frac{1}{4} \times \frac{1}{4}$ or $\frac{1}{16}$
<i>PpBB</i>	$\frac{2}{4} \times \frac{1}{4}$ or $\frac{2}{16}$
<i>PpBb</i>	$\frac{2}{4} \times \frac{2}{4}$ or $\frac{4}{16}$
<i>Ppbb</i>	$\frac{2}{4} \times \frac{1}{4}$ or $\frac{2}{16}$
<i>ppBB</i>	$\frac{1}{4} \times \frac{1}{4}$ or $\frac{1}{16}$
<i>ppBb</i>	$\frac{1}{4} \times \frac{2}{4}$ or $\frac{2}{16}$
<i>ppbb</i>	$\frac{1}{4} \times \frac{1}{4}$ or $\frac{1}{16}$
Totals	$\frac{16}{16}$ or 1

This corresponds to the genotypic ratio found in the F_2 of a dihybrid cross

The probability of any two or more independent events occurring together follows a certain mathematical formula developed by expanding the binomial $(a + b)^n$. The expansion of the binomial to the eighth power is given in Table 6. This formula may be used to determine the probabilities of occurrence of several events, such as the sex ratio of the offspring in families of different sizes and the occurrence of different ratios of genotypes and phenotypes in the offspring from parents of known genotypes

TABLE 6
THE BINOMIAL EXPANDED TO THE 8TH POWER

	<i>Total items</i>
$(a + b)^2 = a^2 + 2ab + b^2$	4
$(a + b)^3 = a^3 + 3a^2b + 3ab^2 + b^3$	8
$(a + b)^4 = a^4 + 4a^3b + 6a^2b^2 + 4ab^3 + b^4$	16
$(a + b)^5 = a^5 + 5a^4b + 10a^3b^2 + 10a^2b^3 + 5ab^4 + b^5$	32
$(a + b)^6 = a^6 + 6a^5b + 15a^4b^2 + 20a^3b^3 + 15a^2b^4 + 6ab^5 + b^6$	64
$(a + b)^7 = a^7 + 7a^6b + 21a^5b^2 + 35a^4b^3 + 35a^3b^4 + 21a^2b^5 + 7ab^6 + b^7$	128
$(a + b)^8 = a^8 + 8a^7b + 28a^6b^2 + 56a^5b^3 + 70a^4b^4 + 56a^3b^5 + 28a^2b^6 + 8ab^7 + b^8$	256

An example of the use of this formula may be shown by the following problem. If a herd of five cows was bred, what would be the probability that all would produce bull calves? We now look in Table 6 for the expansion of the binomial to the fifth power. We shall let the letter *a* represent bull calves and the letter *b* represent heifer calves. We find that the probability of five bull calves from five cows within the herd in the same year is $(\frac{1}{2})^5$ or $\frac{1}{32}$.

Recently a letter was received by the author from a dairyman stating that in a herd of twenty cows he had twenty bull calves and no heifers in a single year. In fact, for several years he had found that almost all calves were bulls. He wanted to know what he could do to produce a larger proportion of heifer calves in this herd. We couldn't give him advice, but it was of interest to calculate the probability that 20 cows in a herd would all have bull calves in a particular year. This probability would be $(\frac{1}{2})^{20}$, or about one chance in a million. The sex ratio he gave would lead one to suspect either that the records were incomplete or that some conditions peculiar to that herd were responsible for the abnormal sex ratio.

The following is another problem which illustrates the use of the expanded binomial. Suppose that, for the herd of five cows, we had asked what the probability would be that three heifers and two bulls would be produced in a given year? Again letting the letter *a* represent the bulls and the letter *b* the heifers, we look for the combination of a^2b^3 . We find the figures $10 a^2b^3$, and, substituting, we have $10 (\frac{1}{2})^2(\frac{1}{2})^3$. Completing the calculations, our final figure is $\frac{10}{32}$. In other words, there is about one chance in three that a herd of five cows will produce three heifers and two bulls in a given year.

The rule of probability can be used to calculate the number of matings necessary to determine whether breeding animals of normal phenotype are homozygous normal or heterozygous for a particular recessive gene. As our problem, let us determine the probability that carriers of the dwarf gene (Dd) mated to dwarf animals (dd) a different number of times would produce all normal calves.¹ The principles involved here would be the same in testing for any recessive gene as long as dominance was complete and penetrance was 100 per cent. The answer to this problem is given in Table 7.

The data presented in Table 7 shows that, as the number of matings of a heterozygote to the homozygous recessive increases, the probability of all calves being normal in appearance becomes less and less. After the production of five normal-appearing offspring from a cross of a questionably normal phenotype to the known homozygous recessive we could conclude that such an individual was probably homozygous normal. The probability of being correct would be about 97 chances in 100. The more offspring of normal phenotype produced, the more confidence we would have that the individual being tested was homozygous normal, although we could never be 100 per cent certain that this was true. In practical application, in a progeny test of this kind, all normal-appearing offspring having one homozygous recessive parent would be carriers of the recessive gene. These, then, could be eliminated from the breeding program

TABLE 7

THE PROBABILITY OF CARRIERS OF A RECESSIVE GENE PRODUCING ALL NORMAL-APPEARING OFFSPRING WHEN MATED WITH HOMOZYGOUS RECESSIVE INDIVIDUALS

Number of Matings	Number of Independent Events*	Probability of Normal Calves	
		In Fractions	In Decimals
1	$1/2^1$	$1/2$.50
2	$1/2^2$	$1/4$.25
3	$1/2^3$	$1/8$.125
4	$1/2^4$	$1/16$.063
5	$1/2^5$	$1/32$.031
6	$1/2^6$	$1/64$.016
7	$1/2^7$	$1/128$.008
8	$1/2^8$	$1/256$.004
9	$1/2^9$	$1/512$.002
10	$1/2^{10}$	$1/1024$.001

*The probability of a single calf from one parent that is heterozygous and the other homozygous recessive is $1/2$. All calves of normal phenotype will be heterozygous for the recessive gene.

TABLE 8

THE PROBABILITY OF CARRIERS OF A RECESSIVE GENE PRODUCING ALL NORMAL-APPEARING OFFSPRING WHEN MATED WITH CARRIERS OF A RECESSIVE GENE

Number of Matings	Number of Independent Events*	Probability of Normal Calves	
		In Fractions	In Decimals
1	$3/4^1$	$3/4$.75
2	$3/4^2$	$9/16$.56
3	$3/4^3$	$27/64$.42
4	$3/4^4$	$81/256$.32
5	$3/4^5$	$243/1024$.24
6	$3/4^6$	$729/4096$.18
7	$3/4^7$	$2187/16384$.13
8	$3/4^8$	$6561/65536$.10
9	$3/4^9$	$19683/262144$.08
10	$3/4^{10}$	$59049/1048576$.06
11	$3/4^{11}$	$177147/4194304$.04

*The probability of a single calf from two carrier parents being of the normal phenotype is $3/4$.

with the confidence that one was eliminating an undesirable character from the herd.

Sometimes it is not practical to use homozygous recessive individuals as testers, because they may not live to maturity or they may be of very low fertility. As an alternative, individuals known to be heterozygous may be used for testing purposes. The probability of carriers of a recessive gene producing all normal-appearing offspring when mated different numbers of times is shown in Table 8. This is the method most often used in testing a bull of unknown genotype to determine if he is a carrier of the dwarf gene. As shown in Table 8, the chances are 4 in 100 that a carrier bull mated 11 times to known carrier cows would produce all normal calves. Thus, when a normal-appearing bull of unknown genotype is mated 11 times to known carrier cows and produces all normal offspring, we can say he is not a carrier of the dwarf gene, with the probability of being right about 96 times in 100. On the other hand, one dwarf calf from one mating would prove him a carrier of the dwarf gene.

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Questions and Problems

- 1 Why do we have a use for the laws of probability in animal breeding?
- 2 What is the rule, or rules most often used in animal breeding for the combining of probabilities?
- 3 Two purebred Black Angus parents produce a red calf. What is the probability that their next calf will be black?
- 4 Using parents in question 3, what is the probability that their second offspring will be a red bull calf?
- 5 Two polled Herefords are mated and they produce a bull calf that is horned. If they are later mated to produce 6 more offspring, what is the probability that all 6 of the calves will be polled? What is the probability that 4 of the calves will be polled and 2 will be horned?
- 6 In progeny testing to determine if an individual is homozygous dominant or heterozygous when is it more practical to use homozygous recessive individuals for the tester animals? When should known heterozygous individuals be used for this purpose?
- 7 A breeder can also use daughters of a known heterozygous bull in order to test for a recessive gene. How many daughters would be required for a test at the 95 per cent level of probability?
- 8 In question 7, would it be permissible to use the same daughter, or daughters, several times in testing a single bull? Explain your answer.

9

Gene Frequencies in Populations

A POPULATION MAY BE DEFINED AS the total of all individuals in a breed, in a species, or in other such groupings or as those individuals which inhabit a particular area. When we speak of population genetics we refer to the study of the genetic composition of one such particular population.

Controlled matings of individuals of known genotypes were used as examples in previous chapters to illustrate certain fundamental principles of Mendelian inheritance, and we learned that one can predict the genotypic ratios that will occur in the F_1 and F_2 generations. In populations of animals where the genotypes of the breeding animals for a particular trait are seldom known, it is more difficult to predict with reasonable accuracy the genotypic ratios of the offspring. Research work in genetics of populations, however, has shown that many of the Mendelian laws of inheritance that operate in individual matings and crosses also apply to populations. This chapter will discuss some of these principles and their application.

GENE FREQUENCIES

The term *gene frequency* refers to the relative abundance or the relative rarity of a particular gene in a population as compared to the other alleles in that particular series. In the example of single-factor inheritance in Chapter 5, where polled bulls (PP) were mated to horned cows (pp), the alleles P and p were introduced into the F_1 in equal numbers. In actual practice, however, this may not occur, and these two genes may be present in the population in ratios quite different from those in the example.

For illustration, let us assume that we own a herd of horned Hereford

cows and have used nothing but horned Hereford bulls for many, many years. The calf crop during this time has never included a naturally polled calf. Under such conditions, the frequency of the horned gene p would be one and the frequency of the polled gene P would be zero. Notice that we assume that the frequency of a gene varies between zero and one. When the frequency of a gene is one, as in this example for the horned gene, the population or herd is completely homozygous for that gene. On the other hand, if the frequency of the polled gene were one, which is very unlikely, the frequency of the horned gene would be zero, and we could say that the herd or population was completely homozygous for the polled gene.

For further illustration of the meaning of gene frequencies, let us make a mating of a homozygous polled bull with homozygous horned cows as follows:

P_1	Polled bull PP	\times	Horned cows pp
F_1	All Pp Polled (<i>inter se</i>)		
F_2	1 PP Polled		
	2 Pp Polled		
	1 pp Horned		

We may now ask what the frequencies of the genes P and p would be in the F_1 . Obviously, all individuals in this generation would possess one gene of each kind, so the frequency of each gene would still be 0.5, since the total of the frequencies of both genes must equal one.

We might also ask what the frequencies of the two genes are in the F_2 . By calculation, we see that in the F_2 there are 4 P and 4 p genes, showing that the frequency of each gene is still 0.5. If we discarded all of the horned animals, however, there would be a total of 4 P genes and 2 p genes left, and the frequency of the two genes would be 0.67 and 0.33, respectively.

definite ratio, or will be in equilibrium in the next generation, at the frequencies of a^2 , $2ab$, and b^2 . From this definition, then, after one generation of random mating, individuals of the genotypes involving the two alleles will occur at the following frequencies:

Number of homozygous dominant individuals will equal a^2 ,
Number of heterozygous individuals will equal $2ab$,
Number of homozygous recessive individuals will equal b^2 .

The use of this law in calculating gene frequencies in a population will be illustrated later.

WHAT IS A RANDOMLY MATING POPULATION?

Before proceeding with the discussion of the calculation of gene frequencies in a population, it is important to discuss more fully one important point in the Hardy-Weinberg Law, i.e., randomly mating populations.

Random mating in a population for a certain character means that matings of individuals are made without attention to their genotype for that trait. Probably one of the best examples of the results of random mating is the frequencies of human blood types involving the M and N alleles. Men and women pay no attention to these blood groups of their prospective spouses. In fact, very few people know what their genotype is for these blood groups, because this information seems to be of little importance from the physiological standpoint.

CALCULATING GENE FREQUENCIES IN A POPULATION

Since the M and N genes for blood types in humans are excellent examples of random mating, and all three genotypes can be identified by a blood test, this trait will be used to illustrate the calculation of gene frequencies.

Three hundred sixty-one Navajo Indians in New Mexico were tested for blood groups, and it was found that 305 belonged to blood group M , 52 to blood group MN , and four to blood group N .¹ Obviously, the occurrence of the three genotypes does not follow a 1:2:1 ratio as would be the case if matings among MN and MN individuals had been made. This does not mean, however, that the M and N blood types do not follow the Mendelian laws of inheritance. Instead it means that the frequency of the N allele is much lower in that group than the frequency of its M allele. This may be demonstrated rather easily by the data in

TABLE 9

FREQUENCY OF M AND N BLOOD GROUPS AMONG NAVAJO INDIANS IN NEW MEXICO

Blood Group	No of Individuals	Number of	
		M Genes	N Genes
MM	305	610	0
MN	52	52	52
NN	4	0	8
Totals	361	662	60

Table 9 Remembering that the sum of the frequencies of the two genes must equal one, and that in the population there is a total of 722 M and N genes, we make the following calculations

$$\text{Frequency of } M \text{ gene} = \frac{662}{722} = 0.918$$

$$\text{Frequency of } N \text{ gene} = \frac{60}{722} = 0.082$$

In many traits in farm animals, however, such as dwarfism in beef cattle and red coat in the Black Angus breed, we cannot tell by visual inspection which animals are heterozygous for the recessive gene. We do have some idea of the proportion of homozygous recessive individuals in the population. By applying the principles of the Hardy Weinberg Law, we can estimate the number and proportion of different genotypes present in the population. The accuracy of these calculations depend upon (1) the size of the population, (2) the correct determination of the proportion of homozygous recessive individuals and (3) the random mating of individuals in the population for at least one generation.

To illustrate the use of gene frequency analysis, let us assume that, in purebred cattle of a certain breed 4 out of every 100 calves dropped are dwarfs. Our problem is to determine the probable frequency of the dwarf gene in this population and the probable frequency of the heterozygous individuals. For the calculations we will refer to the normal allele as D and the dwarf allele as d . Substituting D for a and d for b in the binomial, we obtain the formula $D^2 + 2Dd + d^2$. The frequency, or the proportion of dwarfs in the population would equal d^2 or 0.04, and the frequency of the dwarf gene (d) would be the square root of 0.04, or 0.20. The frequency of the normal gene (D) would be $1 - 0.2$, or 0.8. We can now calculate the frequency of the carrier individuals (Dd) from the formula $2Dd$ and this would be $2(0.8 \times 0.2)$, or 0.32. In other words, 32 out of each 100 of the cattle in the population should be carriers of the dwarf gene.

Records indicate that approximately one Angus calf out of every 200 is red instead of black. Using the same procedure used for the dwarf gene, we find that the frequency of the red gene is the square root of 0.005, or 0.07, and the frequency of the black gene is $1 - 0.07$, or 0.930. The expected frequency of heterozygous black individuals in the population would be 2 (0.07×0.93), or about 13 out of each 100.

Knowledge gained from a gene-frequency analysis may be used to determine the possible mode of inheritance of a particular trait in a population. Probably the most important point about gene frequencies, however, is to realize how changes in gene frequencies are related to selection.

SOME FACTORS WHICH MODIFY GENE FREQUENCIES

The realization that genes vary in the frequency with which they occur in a population leads to the question of why they vary. The following are factors which can be responsible for such variations.

MUTATIONS

Mutations can cause changes in gene frequencies. For example, suppose that a population is completely homozygous for the *A* gene. It is conceivable that, with new generations of individuals being produced, this gene may mutate to *a*. As more generations are produced, it is possible for gene *a* to increase in frequency at the expense of gene *A*. Actually, for mutations to have much effect in changing gene frequencies, they must occur quite often, and there must be a definite selective advantage for the new gene. Under such conditions, it is conceivable that eventually the new allele would largely replace the original one. A point should be reached, however, before the original gene is eliminated, where selection in one direction to eliminate one gene will finally equal the mutation rate in the other, so that the gene frequency in the population would become stable, that is, in equilibrium. This point, where the elimination of a gene becomes equal to its replacement by mutation, is called mutation equilibrium.

Mutation equilibrium may be reached, theoretically, for another reason. It is well known that mutations are reversible, in that there is not only a mutation from gene *A* to *a*, but one from *a* back to *A* again. Furthermore, these reversible mutations are not always equal in their occurrence. If we suppose that before a mutation occurs, the frequency of the *A* gene is 0.80, and that the mutations from *A* to *a* occur twice as rapidly as those in the opposite direction, a mutation equilibrium will eventually be reached. At first, the shift in the gene frequency would be toward a higher level of the *a* allele. Eventually, however, if the frequency

of the *a* allele became twice as great as that of the *A* allele, which mutated at twice the rate, there would be a *status quo* or equilibrium of the alleles in the population.

SELECTION

With respect to farm animals, selection means that individuals possessing certain traits are caused or allowed to reproduce at a more rapid rate than other individuals in the same population. Thus, individuals of a certain genotype are retained for breeding purposes in larger numbers than are others. This causes an increase in frequencies of some genes and a decrease in frequencies of others. Selection has been a very potent force in the past, as shown by the presence of different breeds of sheep, horses, and hogs, and by the different types of dairy cattle and beef cattle. One of the main differences between breeds is that they differ in the frequencies of genes for certain traits.

MIXTURE OF POPULATIONS

When one group of individuals migrates to another part of the country and interbreeds with the natives of that region, a change in the gene frequencies of that population can occur, provided that both groups originally differed in the kinds of genes they possessed for a particular trait. A good example of this is the cattle in the southwestern region of the United States where, several years ago, most of the cattle grown there possessed horns. Later, breeders purchased naturally polled bulls and mated them to the horned cows. The use of the polled bulls increased the frequency of the polled gene and decreased the frequency of the horned gene among cattle in that region.

GENETIC DRIFT

Chance fluctuations of genes may be important, especially in small populations. Wright³ has called this mechanism affecting gene frequencies *random genetic drift*. For example, suppose that from a large herd of cows and bulls, some of which possess horns and some of which are polled, we select one bull and four cows for breeding purposes. If we pay no attention to whether they are horned or polled, it is entirely possible that by chance we might select those which were all horned. The new herd developed from these parents could be quite different from the original population in the frequency of the polled or horned gene. Even in larger populations, genes may become either fixed or entirely lost due to chance. This is particularly true if a particular gene has no selective advantage over its allele.

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Questions and Problems

1. What is a population?
2. Define the term *gene frequency*.
3. What conditions must be met for the Hardy-Weinberg law to be applied to a population?
4. What is the frequency of a gene when all individuals in that population are homozygous for that gene?
5. In a herd of purebred Shorthorns, 100 are red, 50 are roan, and 10 are white. What is the frequency of the red gene in the herd? What is the frequency of the white gene?
6. What factor, or factors, may be responsible for the great difference in the frequency of the red and white genes in this herd?
7. Muscular hypertrophy in cattle is described as a recessive condition in which the thighs are extremely thick and full, with a deep groove between the muscles. In a herd of 1,000 cows, an average of 10 such calves per year are dropped over a five-year period. What is the probable frequency of the gene for this trait in that herd?
8. In problem 7, what is the probable number of normal-appearing carriers of this gene in this herd of 1,000 cows?
9. Explain how genetic drift may be responsible for a change in the frequency of a gene in a population.
10. Explain what is meant by the term *mutation equilibrium*.

10

Mutations

A MUTATION MAY BE DEFINED AS a change in the self-duplication process of a gene so that a new allele is produced which differs from the original gene in its effect upon the expression of a particular trait. Mutations may also be due to a change, or changes in chromosomes (chromosome aberrations), which may change the phenotype. In a gene mutation the new gene duplicates itself exactly for succeeding generations or until another mutation occurs. This is the explanation for the occurrence of several alleles in a multiple allelic series.

Mutations may occur in genes either in the somatic cells or in the germinal cells. Somatic cell mutations are not transmitted from parents to offspring, so they are not of great importance genetically. An example of a somatic cell mutation is the occurrence of a black hair spot on the red portion of the coat of Hereford cattle. If a mutation should occur in the somatic genes for coat color in this breed, it would be dominant since black is dominant to red.

Mutations are responsible for genetic variations in our farm animals. If genes could duplicate themselves perfectly for generation after generation over a period of thousands of years without a single mistake, members of a given species would have the same color, would be alike for the qualitative traits, and would not be divided into distinct types and breeds. All variations that exist would be superficial environmental effects and would not be transmitted from parents to their offspring.

Familiar mutations in farm animals are due to changes in the composition of the genes themselves. In plants and lower forms of animals, however, it is known that mutations also are often due to changes in the chromosomes, and these are called *chromosome aberrations*. Similar mutations must also occur in farm animals, but they have not been identified. Since mutations involving changes in specific genes seem to be of the greatest importance in animal breeding, we will discuss these first.

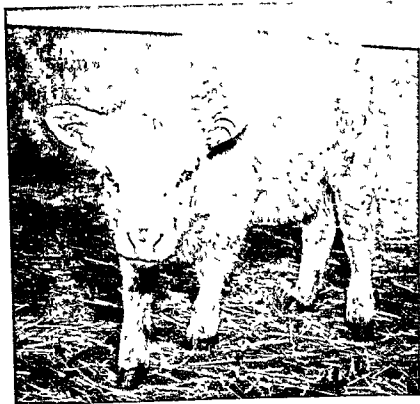


FIGURE 19 ALBINO
HEREFORD DWARF ILLUS-
TRATING THE OCCURRENCE
OF A RARE MUTATION IN
CATTLE. (COURTESY OF
M. E. ENSMINGER, WASH-
INGTON STATE UNIVER-
SITY.)

OCCURRENCE OF MUTATIONS

Many mutations in farm animals have occurred in the past and will continue to occur in the future. References in the Holy Bible show that mutations occurred in humans many years before the birth of Christ, although the reason for their occurrence was not then known. In 2 Samuel 21:20, it is written, "And there was yet a battle in Gath, where was a man of great stature, that had on every hand six fingers, and on every foot six toes, four and twenty in number; and he also was born to the giant." This particular characteristic is now known as polydactyly and is known to be inherited as a dominant trait. It had its origin from a mutation affecting finger number.

One of the first mutations affecting body form in farm animals appearing in American farm records is the case of the Ancon sheep that was mentioned earlier.³ Polled cattle developed from an original mutation of the horned to the polled gene; and the different colors in all of our farm animals probably are the result of mutations from some original color in animals before domestication. Many inherited defects have been reported^{6,7} for the different species of farm animals, showing that a tremendous number of mutations have occurred in the past and are still present in the animal populations in the recessive state.

Research in genetics shows that some genes are more stable than others and that mutations occur in them less often than in others. In humans, it has been estimated² that the rate of new mutations per 100,000 gametes

ranges from 14 to 8. Other estimates⁵ suggest that the total rate of mutations for the 5,000 or more loci assumed to exist in the chromosome entity of humans results in an average of about one new mutation in 10 or fewer gametes. It is also believed that the hidden recessive and semi-dominant load of mutations in the human species may average eight or more per person. If this is true in humans, undoubtedly the same is true in farm animals.

The discovery or the appearance of new mutations depends to a certain extent upon whether they are dominant or recessive in their expression. If they are dominant, they are recognized immediately, but if they are recessive, they may be carried in a population for generation after generation and may not be discovered unless two individuals are mated that carry the same recessive gene. Even then, for any one mating, the chances are only one out of four that a homozygous recessive individual will result. From this we can say that the discovery of a new mutation is dependent entirely upon our ability to measure or observe the expression of a gene that is different from other alleles in that particular series.

IMPORTANCE OF MUTATIONS

Observations made by many geneticists indicate that an overwhelming majority of mutations are recessive, and detrimental to the organism. A few, such as the polled trait in cattle, may be beneficial, but we have to observe a large number of mutations before we find one that is beneficial. In the past, the animal breeder has spent very little time in eliminating harmful mutations from his herd, because he has not recognized them as being very important. The appearance of the condition of snorter dwarfism, in which there must have been some selective advantage for the heterozygous individuals, is an exception; breeders directed much attention to the elimination of this defect. Mutations resulting in defective development of farm animals in which the heterozygote does not have a selective advantage will not become very important in the future unless inbreeding is practiced, but our ideas on this could change as more information on the subject becomes available.

HOW MUTATIONS BECOME ESTABLISHED IN A POPULATION

If most mutations are detrimental and recessive, how do they become established in a population? Mutations have originated initially from a mutation in a single individual, and there are several possible reasons for a gene's increasing in frequency at the expense of its allele or alleles.

One is the rate of recurrent mutation at that particular locus on the chromosome. It was pointed out earlier that genes differ in their rates of mutation, some mutating much more often than others. Thus, a gene that undergoes mutation very frequently would have a better chance of gaining a foothold in a population than would one that mutated much less frequently. Another reason is that the heterozygous individual may be favored by either natural or artificial selection in a particular environment. In such a case, the frequency of the recessive gene would be increased, even though the homozygous recessive individual might not be capable of reproduction. The selective advantage of the heterozygous individuals need not be exceedingly great if the gene mutates frequently and if there is a long period of time for the selection forces to operate. A third reason is that the segregation ratio may be abnormal, with the recessive gene being carried in the gametes more often than normal. As was pointed out by Crow,¹ the short-tailed condition in mice occurs more frequently than expected, and this may be due to some process whereby the gene for this trait segregates in the gametes at a higher rate than is normal or expected.

CHROMOSOME ABERRATIONS

Chromosomes do not always behave in a normal manner in the process of mitosis and meiosis.⁸ They may fail to separate at meiosis, so that the gamete either has an extra chromosome or lacks one. In some instances, whole sets of chromosomes may be duplicated in the gamete. A chromosome may rearrange itself so that the genes may be located in a different order, and this may have a decided effect on the expression of a particular gene. Instead of an entire chromosome being duplicated, only a portion may be involved. In addition, there may be an exchange of parts between two chromosomes which are not homologous. These abnormalities are known as chromosome aberrations (deviations from normal) and may cause decided changes in the phenotype of an individual.

Many chromosome changes have been reported in plants and lower forms of animals, and, as was pointed out in Chapter III, defects such as Mongolism and Klinefelter's syndrome in humans are due to such abnormalities. The importance of chromosome aberrations in farm animals has been given little attention, but this is a promising field of research in the future. Possibly many defects in farm animals are due to some form of chromosome abnormality.

Many different agents are known to cause chromosome aberrations in plants and lower forms of animals. The duplication of entire sets of chromosomes (polyploidy) in some plants, such as tobacco, yeast, and chrysanthemums, has been useful in some instances in producing larger

and more vigorous plants. The principle has not been applied to farm animals and we do not know for certain the possible application to animal breeding. Indications are, however, that the induction of polyploidy in farm animals may not be possible because of accompanying sterility or failure of embryo development.

INDUCTION OF MUTATIONS

Research work with plants³ and with insects⁴ has shown that mutations may be caused by exposure to certain chemicals and X rays. These artificially induced mutations are similar to those which occur under natural conditions. From the study of induced mutations, one important fact has been discovered—that even though the mutation rate can be greatly increased by artificial means, the mutation of a particular gene cannot be controlled at will. That is, one cannot attempt to induce desirable mutations artificially. For the livestock breeder, this means that it is not practical to use X rays and chemicals on breeding stock to induce mutations, for even if this could be done, many defective genes would appear before a favorable mutation was found and defective genes would occur with the favorable ones.

For the present, at least, the livestock breeder can watch for the rare favorable mutations which might occur to cause an improvement in the present-day breeds of livestock. This, however, is going to be much harder than looking for the proverbial needle in a haystack and conceivably is of little or no value in constructive livestock breeding. The more desirable practice is to weed out the detrimental mutations that now exist in our breeds of livestock and to improve existing stocks through proper mating and selection systems, for these have proved to be reliable methods.

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Questions and Problems

1. Explain the meaning of the term *mutation*.
2. What is the mode of inheritance of most mutations? What is the importance of a knowledge of this to the animal breeder?
3. Explain the difference between gene mutations and chromosome aberrations.
4. What is meant by a somatic cell mutation?
5. What causes a new mutation to become established in a population?
6. What is the importance of mutations to the animal breeders?
7. Explain why the artificial induction of mutations in farm animals is of little value at the present time.

11

Detrimental and Lethal Genes in Farm Animals

THE LITERATURE CONTAINS NUMEROUS reports of detrimental genes in farm animals. Some of these genes have such a drastic effect that they cause the death of the young during pregnancy or at the time of birth. Such genes are referred to as *lethal* (deadly) genes. Other genes, which are called *sublethal* or *semilethal*, cause the death of the young after birth or some time later in life. Still other genes do not cause death, but definitely reduce viability or vigor. These will be referred to as *nonlethal* or *detrimental* genes.

WHEN LETHAL OR DETRIMENTAL EFFECTS OCCUR

A lethal gene may have its effect any time from the formation of the gamete until birth or shortly afterward. In a strain of horses, a sex-linked recessive lethal has been reported that kills approximately one-half of the male offspring of carrier females, so there are approximately twice as many females as males at birth. It is possible that such a genetic defect may also be present in other species of farm animals. Frequently a cow or mare is mated, and apparently conceives, because she does not show signs of estrus at the time of the next regular heat period, but returns to estrus at a later date. Possibly conception takes place, but the zygote or embryo dies because of lethal gene effects; it is resorbed, and the female resumes the normal estrous cycle. There is good evidence that lethal genes may cause losses in swine during pregnancy, because inbreeding increases embryonic death losses whereas crossbreeding decreases them. This suggests that genes with nonadditive effects are involved.

The largest proportion of death losses in young farm animals occurs at the time of birth or within a few hours thereafter. Very often, when

the animals also have some obvious external defect, studies have been made to determine whether lethal genes are involved. In many cases they have been found to be responsible, and the mode of inheritance has been determined. When the dead young show no obvious external defects, a possible genetic cause of death is less likely to be investigated.

Many times, lethal genes have their effects on the internal organs. Although such inherited traits have not been fully investigated, we know they must exist, for increased inbreeding is followed by higher death losses in the young from birth to weaning, whereas lower death losses during this period accompany crossbreeding. In fact, in most animals inbreeding and crossbreeding seem to have their greatest effects during this period of life. As was true with embryonic death losses, genes with nonadditive effects must be involved.

Sublethal or semilethal genes are responsible for some death losses in farm animals. Dwarfism in Herefords, resulting from the mating of Comprest with Comprest, is such an example. The dwarfs are born alive, as a general rule, but almost invariably they die before they are one year of age.

Other genes with no obvious visible effects may be detrimental; they express themselves in the reduction of life span or of vigor. Undoubtedly, many of these genes have escaped detection, even though they may be of as great economic importance as those genes with lethal or semilethal effects.

MODE OF EXPRESSION OF LETHAL OR DETRIMENTAL GENES

Most detrimental and lethal genes are either recessive or partially dominant and must be present in the homozygous state to have their full effect. In some instances, the partially dominant genes affect the heterozygous individuals so that they are intermediate in phenotype between the normal and the homozygous recessives.

Detrimental recessive genes are generally present at low frequencies in a population, and, in many cases, only inbreeding or linebreeding will cause their occurrence in the homozygous state. Knowing that homozygous recessives of detrimental genes will appear at greater rates with the practice of inbreeding, breeders have avoided and still avoid it. Because of the low frequency of these genes, breeders direct little effort toward eliminating or controlling their appearance in their herds. Sometimes, however, the frequency of a lethal or detrimental gene may become relatively high, as was the case with snorter dwarfism, which caused considerable economic loss to some breeders of purebred cattle in the 1950's. The frequency of the dwarf gene was so high in many herds that numer-

ous individuals of the homozygous recessive genotype were produced even without inbreeding

COAT COLOR AND DETRIMENTAL GENES

Experiments mostly with small laboratory animals indicate that in some instances genes affecting coat color also affect the vigor of the individual. In mice it is known that coat color is affected by genes located at 24 or more loci on the chromosomes and that many of these genes have highly specific effects on other characters such as skeletal growth and the development of certain body tissues.^{25, 30} One of the first of these effects was found in a certain strain of yellow mice many years ago. When yellow mice were mated they produced approximately two yellow to one nonyellow offspring rather than the 3:1 ratio expected if yellow were dominant and nonyellow were recessive and yellow mice were heterozygous. It was found that homozygous yellow individuals died at an early stage of gestation and the surviving yellow animals were heterozygous. Thus a lethal gene was related to the homozygous yellow color. Platinum foxes are also known to be heterozygous because they produce two platinum to one silver offspring when mated. The homozygous platinum individuals apparently die before birth as a general rule.

Some lethal coat colors have also been reported in farm animals. In sheep of certain gray breeds the mating of gray with gray individuals results in progeny of which one fourth are black and three fourths are gray. This indicates that black is recessive. A large proportion of the gray lambs possess an abnormal abomasum as well as other defects of the digestive tract that causes death within a few months after birth. In horses there is also some evidence that the true albino of the homozygous genotype may die before birth.¹²

Many other examples could be given that suggest a relationship between coat color and some other traits. It is not known for certain whether one gene is having the multiple effect or two or more genes are so closely linked on the same chromosome that only one seems to be responsible. In nearly all instances the color genes having a detrimental effect are either dominant or partially dominant in their phenotypic expression.

EXAMPLES OF DETRIMENTAL AND LETHAL GENES IN FARM ANIMALS

Numerous reports in the literature have described the occurrence of detrimental and lethal genes in farm animals and new reports appear each year. The mode of the inheritance of some of the traits has not been

definitely established, because in some instances only a few affected animals were observed and mating tests to prove the mode of inheritance have not been made. This should be kept in mind when statements are made about the mode of inheritance of any one trait. Sometimes, traits are determined by more than one pair of genes, or by genes that vary in their expression or by genes showing incomplete penetrance. This serves to complicate the situation.

Some traits which are undesirable or lethal will be discussed in the remainder of the chapter. No attempt has been made to make this list complete. The list of references should emphasize the fact that many genetic defects have occurred and that breeders should recognize them when they occur in their herds and flocks. Methods of controlling or eliminating such genetic defects are discussed in Chapter 14.

EXAMPLES IN CATTLE

ACHONDROPLASIA 1

Affected calves have short vertebral columns, inguinal hernia, rounded and bulging forehead, cleft palates, and very short legs. The homozygous dominants are bulldog, the heterozygotes are Dexters, and the homozygous normals are Kerrys. About one-fourth of the bulldog calves are aborted after their death in the sixth to eighth month of pregnancy, following a pronounced accumulation of amniotic fluid in the dam. Similar genes have been observed in the Jersey, Hereford, and British Friesian breeds. The mode of inheritance is partially dominant, requiring two genes to have the lethal effect.^{14,42}

ACHONDROPLASIA 2

This condition has been described in the Telemark cattle of Norway and is similar to the bulldog calf. Affected calves are carried to full term and die within a few days after birth due to respiration obstruction. A similar condition has also been reported in Jerseys, Guernseys, and Ayrshires. The mode of inheritance appears to be recessive.⁵⁷

ACHONDROPLASIA 3

Described in the Jersey breed, the defect is quite variable in expression and is usually, but not always, lethal. Both the axial and appendicular skeleton may be affected. The head is deformed, being short and broad, and the legs are slightly reduced in length. In extreme cases, the calves are stillborn or die soon after birth. One affected calf lived for 14 months, when it was slaughtered. A recessive gene seems to be involved.²²

AGNATHIA

This lethal condition has been reported in Angus and Jersey cattle. The lower jaw is several inches shorter than the upper, and it has been observed only in male calves so it may be a sex linked recessive¹⁸

AMPUTATED

The forelimbs end with the arm or humerus and the hind legs are sometimes present and sometimes absent from the hock down. Cleft palate and hydrocephalus have also been observed. Calves are stillborn or die soon after birth. The defect was observed in Swedish Friesian cattle, and is a recessive⁵⁶

BULLDOG HEAD (PROGNATHISM)

Observed in a grade Jersey herd. The skull is broad, the eye sockets large, the nasal bones short and broad, and the forehead broader than normal. The condition is associated with impaired vision in partial or full daylight. Recessive⁷

CEREBRAL HERNIA

Described in Holstein Friesian calves. The affected calves have an opening in the skull because of a failure of ossification of the frontal bones. The brain tissue protrudes and is easily seen. Affected calves are stillborn or die soon after birth. Probably a recessive⁵⁰

COMPRESS HEREFORDS

An extreme form of compactness in body conformation involving a partially dominant gene. One gene produces a compress individual and two a dwarf, the compress or heterozygote being more or less intermediate in phenotype between the dwarf and normal. The homozygous condition is usually lethal¹¹

CONGENITAL LETHAL SPASMS

Affected calves show a continual intermittent spasmodic movement of the head and neck, usually in the vertical plane. Lethal recessive²⁴

CONGENITAL CATARACT

The lens of the affected calves shows an opaque body beneath the cor

nea. The cornea usually becomes enlarged as the animal grows older and becomes distorted in shape. Vision is somewhat reduced. Nonlethal recessive.²³

CURVED LIMBS

A lethal character reported in Guernsey cattle. The hind legs are grossly deformed, with the hocks held close to the body and scarcely flexed forward. Probably a recessive.²¹

DODDLER CATTLE

Affected calves suffer extreme muscle spasms, convulsions, nystagmation, and dilation of the eyes. Respiratory movements are uncoordinated and difficult. A lethal recessive.²⁸

DUCKLEGGED CATTLE

Observed in grade Herefords. The body is of normal size, but the legs are greatly shortened. Probably dominant and nonlethal.³⁷

EPILEPSY

Symptoms are the lowering of the head, chewing of the tongue, foaming at the mouth, and finally a collapse into a coma. Attacks occur at irregular intervals and are usually brought on by undue excitement. Dominant.²

FLEXED PASTERNS

A semilethal condition in Jersey cattle in which the toes of the front feet in some cases are completely turned under. The toes of the hind feet are not affected. Affected calves are as vigorous as their normal sibs, but severely afflicted calves cannot nurse without aid. The abnormality is present at birth and persists for a few days or a week but gradually disappears. Recessive.^{3,41}

HARELIP

Described in Shorthorn cattle. Affected calves are unilaterally hare-lipped, and the dental pad on that side is missing, but the hard palate is formed. Young calves so affected experience difficulty nursing. Epistaxis may be involved.⁵⁵

HAIRLESSNESS

This condition has been described in several breeds, but it is not known if it is determined by a recessive gene at the same locus. There is variation from partial to almost complete lack of hair. Most reports indicate that it is due to a recessive gene.³²

HYDROCEPHALUS

Affected calves have a bulging forehead and enlargement of the cranial vault. The limbs and other bones are sometimes involved. It has been described in several breeds, and more recently in the Hereford. The trait is lethal in most cases and is recessive.¹³

HYPOPLASIA OF THE OVARY

An underdeveloped condition of the gonads in both sexes. When both gonads are involved, the animal is sterile, and when one is involved, the animal is less fertile than normal. A recessive gene with reduced penetrance seems to be the cause.¹⁹

IMPACTED MOLARS

Described in milking Shorthorns. Impaction of the premolar teeth in the mandible, which is greatly reduced in length and width, giving a parrot mouth appearance. The calves die within the first week after birth. Recessive.²⁷

LONG-HEADED DWARF

Body proportions are similar to those of the snorter dwarf, but with advancing age the head becomes longer and narrower. Seems not to be due to the gene that causes snorter dwarfism. Recessive.⁶

MULTIPLE LIPOMATOSIS

A large growth, consisting of adipose tissue in the perineal area, appears at about 3.5 years of age and becomes progressively larger. In some cases, the fat deposition invades the udder and prevents the mammary system from functioning normally. It occurs in both males and females and appears to be a dominant gene with complete penetrance.⁴

MUSCLE CONTRACTURE

The limbs are bent, and the joints are rigid and ankylosed. The head is stiff and drawn up toward the back. Recessive lethal.²⁹

MUSCULAR HYPERTROPHY

Described in a crossbred Africander-Aberdeen Angus line. The thighs are extremely thick and full, with a deep groove between the *vestus lateralis* and *semi-membranus* muscles. Affected animals often assume an unusual stance, with the fore and rear legs extended anteriorly and posteriorly. Appears to be due to a recessive with variable expressivity. The heterozygotes appear to be favored in selection.³³

POLYDACTYLISM

Individuals with extra toes on one foot or all feet have been reported in several breeds. The trait is sometimes accompanied by lameness and therefore is undesirable. The mode of inheritance is not clear, but a dominant gene may be involved.⁴⁷

PROLONGED GESTATION

Gestation is prolonged to 310 to 315 days, with calves weighing from 110 to 168 pounds at birth. Calves are thought to be homozygous for a lethal recessive gene.⁴³

SEMI-HAIRLESSNESS

Hair is absent from the margin of the ears and along the underline from the brisket to the udder, on the inside of the legs, the side of the neck, shoulder vein, sides and thighs. Recessive.¹⁵

SCREWTAIL

This trait is caused by a fusion of one or more pairs of the coccygeal vertebrae at the end of the tail. Some calves show a double and some a single kink. Nonlethal recessive.³⁵

SHORT SPINE

The vertebral column is shortened to about one-half the normal length. Calves are stillborn or die shortly after birth. Recessive.⁴⁴

SNORTER DWARFISM

Dwarf calves are usually thick and blocky at birth, and the difference between dwarfs and normals becomes more noticeable with increasing age. Dwarfs have difficulty in breathing, hence the name "snorter." The same gene is present in both the Angus and Hereford and possibly in the Shorthorn. It may also be present at a low frequency in other breeds. Semilethal recessive.²¹

STRABISMUS

The eyes of affected animals are crossed, and protrude abnormally. The trait is not evident at birth, but develops at 6 to 12 months of age. Recessive.⁴⁶

STUMPY

Affected individuals have curly hair coats, the tail switch is smaller than normal in amount and length, and achondroplastic conditions are more apparent in the fore than in the rear legs. Nonlethal recessive.⁵

SYNDACTYLISM

Individuals have one rather than two toes on one or more of their feet. Probably recessive.¹⁷

UMBILICAL HERNIA

Described in Holstein Friesian cattle. The hernia appears at the age of 8 to 20 days and persists until the calves are 7 months of age. At that time the hernial sac seems to contract, permitting the hernial ring to close. Appears to be limited to males and is dominant.⁵³

WHITE HEIFER DISEASE

Observed in white dairy Shorthorn heifers. The hymen is constricted, the anterior vagina and cervix are missing, and the uterine body is rudimentary. Sex limited recessive gene seems to be involved.⁵¹

WRYTAIL

A malformation resulting in the distortion of the tail head, with the base of the tail being set at an angle to the backbone instead of in line with it. Found in several breeds. Recessive.¹

EXAMPLES IN HORSES

ABRACIA

This term refers to the absence of the fore limbs, and was observed in an inbred line. Probably a recessive lethal.³⁹

ANIRIDIA

Characterized by the absence of the iris, with secondary cataracts. Observed in the Belgian breed. Dominant.²⁰

ATRESIA COLI

A condition resulting from the closure or partial closure of the ascending colon in the region of the pelvic flexure. Observed in inbred Percherons. Lethal recessive.⁵⁷

BLEEDING

The presence of fragile blood vessels in the nasal mucosa, which have a tendency to burst. Has been observed in the English Thoroughbred. It is a semilethal condition and seems to be recessive.⁵⁷

EPITHELIO-GENESIS IMPERFECTA

Foals are born alive, but the hair coat is lacking in some areas of the body. Sometimes a hoof is missing. All foals die within a few days of birth. Recessive.³⁶

FREDERIKSBORG LETHAL

Attempts to propagate a small group of rare white horses in Denmark led to inbreeding and apparently the dissolution and disappearance of the breed. It was suggested that a lethal recessive factor caused the death of the fetuses.⁵⁷

HEREDITARY FOAL ATAXIA

This has been reported in a German breed, the Oldenburg. Symptoms appear at 3 to 8 weeks of age. Affected animals first show periodical failure of muscular coordination or irregular muscular action, then collapse. Death occurs in 8 to 14 days after the symptoms become evident. Recessive.³⁴

SCROTAL HERNIA

This trait appears to be due to an incompletely dominant gene with low penetrance ⁵²

UMBILICAL HERNIA

Reported as a simple recessive trait.²⁶

WRYNECK

A contraction of the cervical muscles results in a twisted neck and unnatural position of the head. One form may not be inherited, but a congenital condition in foals is inherited as a lethal recessive ³⁵

EXAMPLES IN SHEEP**AMPUTATED**

The legs are missing at the fetlock joints in new born lambs. Mode of inheritance not established ³⁸

DWARFISM

Parrot mouth dwarfs have been observed in a strain of Southdown sheep. All lambs affected die within a month of birth. Semilethal recessive ⁹

LETHAL GRAY

The homozygous gray individuals appear to die either during embryonic life or early in postnatal life. The gray color is apparently due to a partially dominant gene ¹⁶

MUSCLE CONTRACTURE

The limbs are rigidly fixed in many abnormal positions at birth with only a small amount of movement possible in the joints. This often makes parturition difficult. The lambs are nearly always dead at birth. Lethal recessive ⁴⁸

EXAMPLES IN SWINE**ATRESIA ANI**

A congenital condition resulting in the lack of an anus in both sow and boar pigs. Male pigs die within 2 or 3 days after birth, whereas sow

pigs sometimes live and reproduce. An opening of the colon into the vagina in sow pigs allows defecation to take place through the vulva. The condition has been observed in several different breeds. It has been suggested that two pairs of dominant genes (epistasis) is involved, but other modes of gene expression and other genes, as well as environment, may be involved.⁸

HAIR WHORLS

Whorls of hair appear on different parts of the body. This condition is undesirable but is not lethal. Two pairs of dominant genes (epistasis) seem to be involved.⁴⁵

HEMOPHILIA

The failure of the blood to clot has been observed in some animals within an inbred Poland line at about 2 months of age. The abnormality appears to increase in severity as the pigs grow older. Some boar pigs that were castrated late in life bled to death. Semilethal recessive.¹⁰

HYDROCEPHALUS

Affected pigs are born dead or die within a day or two. Lethal recessive.⁵⁴

MULE FOOT

A condition in swine where the hoof is solid, as in the mule. Nonlethal dominant.⁴⁰

PARALYSIS

The hind legs are affected, and the pigs crawl only by means of the fore legs, which are less affected. All pigs die within a few days. Recessive.⁸

RED EYES

Observed in Hampshire swine which also had a light brown or sepia hair coat. Not lethal, but undesirable, because Hampshires are black with a white belt. Probably a recessive.⁴⁹

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Questions and Problems

- 1 What is meant by lethal genes?
- 2 Are lethal genes usually dominant or recessive? Explain

3. At what time during life do lethal and sublethal genes express themselves?
4. Why is the mating of related individuals often associated with the occurrence of lethal or detrimental traits in *farm animals*?
5. What is indicated about the frequency of an undesirable gene when it is often expressed by the mating of non-related individuals? Explain.
6. How important are lethal and undesirable genes in animal breeding? Why?

12

Quantitative Inheritance and ✓ Its Measurement

THE DISCUSSION OF THE DIFFERENT types of gene action in Chapters 5 and 6 showed that the expression of some inherited traits is governed by only one or two pairs of genes, whereas that of others is governed by many pairs. The former type of inheritance is referred to as *qualitative* and the latter as *quantitative inheritance*. In qualitative inheritance, a small number of genes is involved, and there is a definite and sharp distinction between the different phenotypes. Coat color in Angus cattle is a good example, all animals being either black or red.

In quantitative inheritance, many pairs of genes are involved, and there is no sharp distinction between the different phenotypes, the differences being ones of degree only. Many traits in farm animals which are of the greatest economic importance are good examples of this kind of inheritance, including fertility, rate of gain, efficiency of gain, milk production, and carcass quality. The expression of these traits is affected by many pairs of genes as well as by environment.

HYPOTHETICAL EXAMPLE OF QUANTITATIVE INHERITANCE IN FARM ANIMALS

For an example of quantitative inheritance, let us use backfat thickness in swine. Actually, many pairs of genes may be involved in the expression of this trait, and their action may be nonadditive as well as additive in nature. In addition, each gene may not contribute equally to the control of production of backfat. Environment can also play a very important part in the expression of this trait. However, for the sake of simplicity, we shall use only two different pairs of alleles, and we shall assume that each contributes equally toward backfat thickness.

Let us assume that the residual genotype is 0.80 inches of backfat thickness, since it has been suggested³ that this probably is the least amount of backfat, from the genetic standpoint, that we can expect to obtain in pigs at the usual market weight of 200 to 225 pounds.

The following information will be used in this example:

B and *F* are contributing genes which add 0.20 inches of backfat thickness in swine.

b and *f* are neutral genes which add nothing.

bbff is the residual genotype, with 0.80 inches of backfat.

P_1	<i>BBFF</i> 1.60 inches	×	<i>bbff</i> 0.80 inches
F_1	<i>BbFf</i> (inter se) 1.20 inches		
F_2	Genotypes	Phenotypes	
	1 <i>BBFF</i>	1.60 inches	
	2 <i>BBFf</i>	1.40 "	
	1 <i>BBff</i>	1.20 "	
	2 <i>BbFF</i>	1.40 "	
	4 <i>BbFf</i>	1.20 "	
	2 <i>Bbff</i>	1.00 "	
	1 <i>bbFF</i>	1.20 "	
	2 <i>bbFf</i>	1.00 "	
	1 <i>bbff</i>	0.80 "	

The phenotypic ratio in the F_2 would be

1	1.60 inches	
4	1.40 "	Mean = 1.20 inches
6	1.20 "	Variation = 0.80 to 1.60
4	1.00 "	
1	0.80 "	

As shown in Figure 20, the F_2 individuals form a normal frequency-distribution curve.

Let us look at the results of these crosses. Notice that the mean of the F_1 offspring was 1.20 inches in backfat, which coincides exactly with the mean or average of the two parents, and that the variation of individuals from this mean is zero. Considerable variation is noted, however, in the F_2 individuals, with a range from 0.80 to 1.60 inches. But when we calculate the mean for the F_2 individuals, we find that it also is 1.20 inches, the same as in the F_1 . This is an excellent example of how two means may be the same but the individuals within the population may vary widely in one instance and not at all in another.

In actual practice, the instances would be rare where the results were as perfect as those in the example above. One reason is that, in selecting

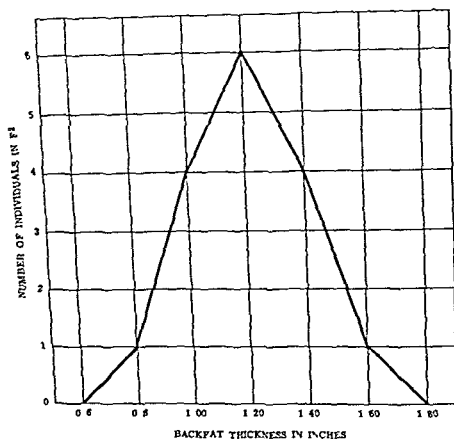


FIGURE 20 ILLUSTRATION OF HOW THE PHENOTYPIC RATIO OF THE DIHYBRID CROSS INVOLVING ONLY ADDITIVE GENE ACTION AND NO ENVIRONMENTAL EFFECTS FORMS A NORMAL FREQUENCY DISTRIBUTION CURVE.

individuals for the P_1 mating it would be difficult, if not impossible, to find those that were homozygous for contributing genes or neutral genes. The trait will have been affected by environment, sex, and amount and kinds of feed, as well as other factors. These other effects would be confusing in the other generations as well. Another important factor, in practice, is that often the mean of the F_1 individuals does not coincide exactly with that of the parents, but may be closer to the mean of one or the other parental group. Many times, of course, this could be due to chance fluctuations but at other times it may actually be a real observation.

In practice, the fact that the mean of the F_1 does not coincide with the mean of the parents would indicate that the genes involved contribute their effects through certain kinds of interactions rather than in an additive manner. Instead of adding or subtracting constant amounts, they seem to multiply or divide the deviation from the residual genotype by some constant amount. As a result, the mean of the F_1 population is closer to the geometric mean than to the arithmetic mean of the parents. The geometric mean is the square root of the product of the parental means.

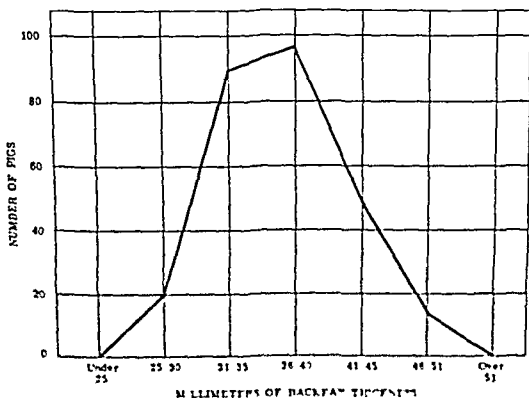
If genes act in a multiplicative manner in affecting a quantitative trait, any deviation of the F_1 from the geometric mean of the two parental groups would indicate that dominance and epistasis are involved

Evidence is now accumulating that additive gene action alone is not responsible for the inheritance of quantitative characters, but that other types of gene action such as overdominance, dominance, and epistasis may also be important. Furthermore, environment is an important cause of variation in most traits. The determination of the relative influence of each of these different kinds of gene action and of environmental factors on economic traits in livestock would be helpful in devising the most effective mating and selection systems.

ACTUAL EXAMPLE OF QUANTITATIVE INHERITANCE IN FARM ANIMALS

Backfat thicknesses of 270 pigs, measured at a market weight of 200 pounds, are presented graphically in Figure 21. Note that these figures assume the bell shaped frequency distribution curve that is characteristic of quantitative traits in a population. In this actual example, environment, as well as heredity, has caused variations. For backfat thickness as well as for other traits, the environmental effects may be very large, and the

FIGURE 21 ILLUSTRATION SHOWING THE DISTRIBUTION OF BACKFAT THICKNESS AT 200 POUNDS LIVE WEIGHT IN 270 PIGS



breeder must control them as much as possible. For instance, animals to be compared should be given the same kind and amount of food. For factors that cannot be controlled, such as age and sex, adjustments should be made in the figures. The methods for making such adjustments will be discussed in each chapter on each of the species.

STATISTICAL METHODS FOR MEASURING QUANTITATIVE TRAITS

Since, in quantitative inheritance, the phenotypes are not distinct and separate but exhibit a series of variations between the extremes, mathematical methods have been devised for measuring and describing populations. Some of these methods will now be discussed, using the backfat thickness of 10 pigs picked at random in the population of 270 pigs recorded in Figure 21.

THE MEAN

Everyone has calculated averages, or means, so little time will be spent on this particular statistical measurement. Nevertheless, to help the student to become familiar with the use of symbols and formulas, the mean may be stated as follows:

$$\bar{X} = \frac{\Sigma X}{n}$$

Many statisticians refer to the mean for a group of individual observations as bar X or \bar{X} . The symbol X refers to each individual item or observation, and the Greek symbol Σ means to add all items in the group. The letter n refers to the number of X items in the group of data to be summed. Using data tabulated in Table 10, we substitute in the formula and calculate the mean backfat thickness of the 10 pigs:

$$\bar{X} = \frac{385}{10} = 38.5 \text{ millimeters}$$

The mean summarizes all values into a single figure that is typical of the entire set of figures in that it is intermediate among the individual values. If successive samples of backfat thickness in groups of 10 pigs were taken from the data in Figure 21, we would find that the means of the different samples of 10 would vary less than do the individual figures. This is one of the reasons why means are used to describe groups of individuals in a population.

THE RANGE

The range is a very rough measure of the variation within a population. It is determined by finding the lowest and the highest values within a series or group of figures. The range of the items in Table 10 is from 31 to 47 millimeters, and this is the most extreme variation possible in this group of data. The chief disadvantages of the range as a measure of variation are that it is subject to chance fluctuations and that it becomes larger as the size of the sample increases. For instance, the range in back fat thickness in the entire 270 pigs included in Figure 21 was from 25 to 51 millimeters, which is considerably larger than the range of the small sample of 10 pigs given in Table 10.

THE VARIANCE

The variance is usually denoted by the symbol (σ^2) and is defined as the average of the squared deviations from the mean. In Table 10 the deviation of each observation from the mean was determined (column 2), each deviation was then squared (column 3), and all the squared deviations totaled. The sum of the squared deviations from the mean is 240.50.

A frequent question is why don't we simply use the average of the deviations from the mean as a measure of variation? One obvious answer

TABLE 10

BACKFAT THICKNESS IN LIVE PIGS MEASURED AT A MARKET WEIGHT OF
APPROXIMATELY 200 POUNDS
(A sample from those in Figure 21)

<i>Backfat Thickness in Millimeters</i>	<i>Deviations from the Mean</i>	<i>Squares of the Deviations</i>
47	8.50	72.25
38	-0.50	0.25
39	0.50	0.25
32	-6.50	42.25
34	-4.50	20.25
37	-1.50	2.25
31	-7.50	56.25
43	4.50	20.25
41	2.50	6.25
43	4.50	20.25
ΣX 385		
ΣX^2 15063		
\bar{X} 38.50	0.00	240.50

is that, when we add all of the deviations and pay strict attention to the sign of each deviation the sum is equal to zero. Thus, the average of the deviations from the means would be zero also. The difficulty could be eliminated, however, by disregarding signs, and if this were done, the average of the deviations in our example would be 4.10 millimeters. Another, and probably more important reason for squaring the deviations and averaging them is to magnify, or give more weight to, extreme values in the group of observations. Squaring the deviations and averaging them also makes it possible to perform other statistical measurements in a correct mathematical manner.

The variance (σ^2) once the sum of the squared deviations from the mean is determined, may be calculated easily by dividing by the number one less than the total number of observations in the sample. Here, another departure from the usual is noted. Instead of dividing by the number of individuals in a sample n we divide by the total minus one ($n - 1$) at least for samples that include less than 25 observations.

The calculation of the variance (σ^2) from the data in Table 9 would be

$$\sigma^2 = \frac{240.5}{9} = 26.72$$

If we were to calculate the variance for a group of 200 to 300 pigs as we have done for the small sample of 10 pigs it would be very time-consuming and the chances for error would be greatly increased. Short-cuts have been devised by statisticians in which the variance may be determined by using a calculator. By using the following equation, the variance could be calculated.

$$\sigma^2 = \frac{\sum X^2 - (\sum X)^2/n}{n - 1}$$

Where $\sum X$ is the sum of all items, $\sum X^2$ is the sum of all items squared, and n is the number of observations in the sample.

Substituting we get

$$\sigma^2 = \frac{15063 - (1285)^2/10}{9} = \frac{240.5}{9} = 26.72$$

By using the calculator we could, of course, obtain the answer more quickly.

One other important point to mention here is that the numerator of the formula for the variance,

$$\sum X^2 - \frac{(\sum X)^2}{n}$$

actually is the sum of the squared deviations from the mean and is often written as Σx^2 . The sum of little x squared divided by the number of observations minus one is the variance.

One of the most useful properties of the variance is that it can be separated by a special analysis into its various component parts. Special adaptations of the analysis of variance can be used to determine the percentage of the variation in a population that is due to inheritance and that due to environment. Many other uses can be made of the analysis of variance, but it is not the purpose here to discuss all of them.

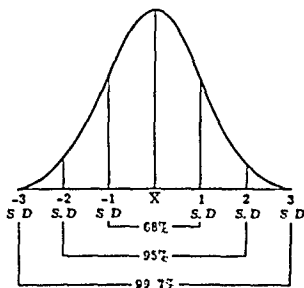
THE STANDARD DEVIATION

The standard deviation is a much more accurate measure of variation in a population than is the range, and can be used very effectively, together with the mean, to describe a population. Statisticians use various symbols to denote the standard deviation, but the one used here will be $S D$. The standard deviation is the square root of the variance. The following formula may be used for machine calculation:

$$S D = \sqrt{\frac{\Sigma X^2 - (\Sigma X)^2/n}{n - 1}} = \sqrt{\frac{\Sigma x^2}{n - 1}} = \sqrt{26.72}, \text{ or } 5.17$$

Figure 22 demonstrates how the mean and the standard deviation may be used to describe the variation in a population. The mean plus or minus one $S D$ should include approximately 68 per cent of the individuals in the population. The mean plus or minus two $S D$ should include about 95 per cent of the individuals in a population. In other words, we might expect only about five per cent of the individuals in a population to fall outside the mean plus or minus two $S D$.

FIGURE 22 NORMAL FREQUENCY DISTRIBUTION CURVE SHOWING HOW THE MEAN AND STANDARD DEVIATIONS MAY BE USED TO DESCRIBE THE VARIATION IN A POPULATION



THE COEFFICIENT OF VARIATION

The coefficient of variation is another method of expressing the amount of variation within a particular population. The Formula is SD / \bar{X} . When this coefficient is multiplied by 100, it is expressed as a percentage. The coefficient of variation is the fraction or percentage that the standard deviation is of the mean. One important use of this statistic is that it can be used to compare the variations of two unrelated groups. For instance, if the coefficient of variation for rate of gain in beef cattle is 25 per cent and in hogs is 15 per cent, we can say that there was a greater variation in daily gains in cattle than in hogs. Many other groups may be compared in a similar manner.

STANDARD DEVIATION OF THE MEAN

In experimental work with livestock, we do not use an unlimited or indefinite number of animals. Actually, we use a very small sample of the entire population. This is true even if our sample includes the hundreds of animals for a given experiment. The question then arises as to how closely the mean of the sample we measure represents the true mean of the entire population. If we assume that the 270 pigs shown in Figure 21 were the entire population, and we take 27 different samples of 10 pigs each at random and determine their mean, each group would probably have a different mean. But the means of the 27 different groups of pigs would have a definite characteristic we have already noted in individual samples within the population—they would tend to fluctuate around a mean of their own. If we plotted them as a frequency distribution, we would find that they also would fall into a normal frequency-distribution curve. This very fact leads us to a method of calculating approximately the true mean of the population and this statistic is called the Standard Deviation of the Mean (S.E.). The standard deviation of the mean may be determined by dividing the standard deviation of the distribution (S.D.) by the square root of the number of items in the population. The formula can thus be written

$$S.E. = \frac{S.D.}{\sqrt{n}}$$

We can use the standard deviation of the mean together with the mean of the distribution to describe the true mean of an infinite number of means drawn from a population. The mean of the distribution plus or minus one S.E. should include about 68 per cent of the means. The mean of the distribution plus or minus two S.E. should include approximately 95 per cent of the means. In other words we can say that there are only 5 chances out of 100 that the true mean of an infinite number of means

drawn from a population would fall outside the mean of a sample plus or minus two S.E. Quite often in scientific reports, the mean of a sample is reported together with plus or minus the S.E.

If the means of two large samples have been derived independently, the information can be used to determine the Standard Deviation of a Difference of means.¹ The formula for this is:

$$\sqrt{(\text{S.E.}_1)^2 + (\text{S.E.}_2)^2}$$

If a difference between the means of two samples is at least twice as large as the Standard Deviation of the Difference, we can accept this as a true difference at the five per cent level of probability.

COEFFICIENT OF CORRELATION

This statistic and the expansion of the idea are often used in animal breeding and livestock production research. The coefficient of correlation is referred to as r and gives a measure of how two variables tend to move together. They are said to be positively correlated if they tend to move together in the same direction; that is, when one increases the other increases, or when one decreases the other decreases. They are said to be negatively correlated if they tend to move in opposite directions; that is, when one increases the other decreases. Thus, the coefficient of correlation for two variables lies somewhere between zero and ± 1 .

Even though the coefficient of correlation tells us how two variables tend to move together in like or in opposite directions, it does not necessarily mean that the movement of one is the cause or the effect of the movement of the other. The cause and effect relationship must be determined, if possible, from other known facts concerning these two variables.

A particular coefficient of correlation is usually said to be significant, highly significant, or nonsignificant, the degree of significance depending upon the size of the coefficient of correlation and the number of individual items used to calculate it.

The formula for calculating the simple coefficient of correlation between two variables is:

$$r = \frac{\Sigma XY - \frac{(\Sigma X) \cdot (\Sigma Y)}{n}}{\sqrt{\Sigma X^2 - \frac{(\Sigma X)^2}{n}} \cdot \sqrt{\Sigma Y^2 - \frac{(\Sigma Y)^2}{n}}}$$

where X is each individual observation for variable X , Y is each individual observation for variable Y , n is the number of observations for each variable, and the Greek symbol (Σ) means the summation of all items for each variable or pair of variables.

TABLE 11

BACKFAT THICKNESS AT 200 POUNDS LIVE WEIGHT AND RATE OF GAIN FROM WEANING TO 200 POUNDS IN 10 MARKET HOGS

Number of Pig	Thickness of Backfat (X)	Rate of Gain (Y)	Cross Products (X times Y)
1	47	2 0	94 0
2	38	1 7	64 6
3	39	1 8	70 2
4	32	1 7	54 4
5	34	1 8	61 2
6	37	1 8	66 6
7	31	1 7	52 7
8	43	1 6	68 8
9	41	1 4	57 4
10	43	1 8	77 4
ΣX 385		ΣY 17 3	ΣXY 667 3
ΣX^2 15063		ΣY^2 30 15	
\bar{X} 38 50		\bar{Y} 1 73	

The coefficient of correlation will be calculated for the data presented in Table 11, as an example. Backfat thickness at 200 pounds (variable X) is the same as that given in Table 10, the rate of gain from weaning to 200 pounds for these same pigs has been included as a second variable (variable Y). Looking at the data in this table, we may ask if these two variables tend to move in like or in opposite directions and if the correlation coefficient is large enough to be statistically significant. All data necessary to calculate the coefficient of correlation are given in Table 11, and we merely substitute the appropriate figures for the symbols in the formula and proceed with the calculations as follows:

$$\begin{aligned}
 r &= \frac{667.30 - \frac{(385)(17.3)}{10}}{\sqrt{15063 - \frac{(385)^2}{10}} \sqrt{30.15 - \frac{(17.3)^2}{10}}} = \frac{667.30 - 666.05}{\sqrt{240.5} \sqrt{0.22}} \\
 &= \frac{1.25}{15.51 \cdot 0.469} = \frac{1.25}{7.27} = 0.172
 \end{aligned}$$

According to tables for the levels of significance of coefficients of correlation given in Snedecor's book (fifth edition)² on page 174, a coefficient of correlation with 8 degrees of freedom ($n - 2$) should be 0.632 to be significant at the 5 per cent level and 0.765 to be significant at the 1 per cent level of probability. Thus, this coefficient of correlation of 0.172 is so small that it is very likely a chance correlation.

THE REGRESSION LINE

Individual paired observations, such as backfat thickness and rate of gain for each pig in Table 11, may vary quite widely from others within a group of observations. In spite of this, however, a line can be calculated which will show the average relationship between two variables. This is called the regression line and is represented by the equation $Y = a + bX$.

The value b in this equation may be calculated as follows

$$b = \frac{\Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}}{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}$$

The regression coefficient b from the data in Table 11 would be

$$b = \frac{667.3 - \frac{(385)(17.3)}{10}}{15063 - \frac{(385)^2}{10}} = \frac{1.25}{240.50} = 0.0052$$

The value b also refers to the slope of the regression line or the number of units change in Y with each unit change in X . Thus, for each change of 1 millimeter of backfat at 200 pounds, there was an average change of 0.0052 pounds in average daily gain.

The value a in the regression equation is called the Y intercept, because the regression line will cross the Y axis at this point when X is equal to zero. The Y intercept for the data in Table 11 may be calculated using the following equation

$$a = \bar{Y} - b\bar{X} = 1.73 - (0.0052 \times 38.5) = 1.53$$

The regression equation, then, becomes $Y = 1.53 + 0.0052 X$. Two regression lines are possible when two variables are concerned, but the choice of the one to calculate and use depends upon which one seems to be dependent upon the other.

The regression equation as shown above may be used to estimate the value of Y when any value of X is known and substituted in the equation.

The above methods of deriving statistical ways to describe the distribution of individuals within a population are simple and can be calculated by anyone. There are many other aspects of statistics, however, that can be used in biology. These include methods for the determination of probable differences between means, methods of determination of both environmental and genetic correlations between two or more traits, and

methods of separation of the variance of a population into its genetic and environmental portions. These methods necessarily require a wider knowledge of mathematics and statistics and for that reason are not presented here. An understanding of these methods of statistical analysis is indispensable for the student who wishes to pursue further advanced studies and research in genetics and animal breeding. Some references for advanced study in the field are given at the end of this chapter.

References

- 1 CRAMPTON, E. W. Estimating Statistically the Significance of Differences in Comparative Feeding Trials. *SAg* 13:16, 1932.
- 2 SNEDECOR, G. W. *Statistical Methods* (5th ed.) (Ames, Iowa: Iowa State College Press, 1956).
- 3 THOMSEN, N. R. Pig Breeding and Progeny Testing in Denmark. in *Report of the Meeting on Pig Progeny Testing in Denmark*. FAOUN, EAAP, pp. 9-12, 1957.

References for Further Study

- DICKERSON, G. E. *Techniques for Research in Quantitative Genetics*. ASAP (monograph) p. 57, 1959.
- FALCONER, D. S. *Introduction to Quantitative Genetics* (New York: The Ronald Press Company, 1960).
- FISHER, R. A. *Statistical Methods for Research Workers* (Edinburgh: Oliver and Boyd, 1950).

Questions and Problems

- 1 List the important differences between qualitative and quantitative inheritance.
- 2 In a feeding trial the rates of gain per day of 10 different steers in one lot were 1.50, 3.60, 3.00, 3.80, 1.55, 2.60, 2.10, 3.20, 1.80, and 2.70. Calculate the mean, standard deviation, coefficient of variation, and the standard deviation of the mean for this group.
- 3 Why is the range a poor way to express the variation of individual observations within a population?
- 4 What is the variance for the group of individuals in question 2?

5. Why do we use the value $(n - 1)$ instead of (n) in calculating the variance?
6. Explain in detail how the mean of a population together with a standard deviation may be used to describe a population.
7. Explain the meaning of the coefficient of correlation.
8. Explain the meaning of the coefficient of regression.

13

Variations in Economic Traits ✓ in Farm Animals

VARIATION REFERS TO THE OBSERVABLE or measurable differences in individuals for a particular trait. This is the raw material with which the animal breeder must work. If there were no variations between individuals, there would be no need to select or cull animals for breeding purposes, because they would all look and perform alike, or at least there would be little difference between them.

The variations we see between animals in a herd are seldom, if ever, due completely to differences in genes. In animal breeding, we must learn ways of determining something about the genetic variation which exists in a population, for if none exists there would be no progress made in selection and breeding. This chapter deals with the causes of variations and how we can estimate more effectively the portion of the total variance that is due to genes.

CAUSES OF PHENOTYPIC VARIATION IN FARM ANIMALS

All phenotypic variations in farm animals are due to heredity, environment, or the interaction of both. The importance and influence of each of these factors will be discussed separately.

HEREDITY

The hereditary portion of the phenotypic variation in an economic trait in a population is called the *hereditary variance* and may be denoted by the symbol (σ_H^2). Hereditary variations in a population are due to differences in the kinds of genes with which the individual begins its life. Although the way these genes express themselves may change at different periods of the animal's life, its genotype is fixed at conception and re-

FIGURE 23 EXTREME VARIATION IN THE SIZE OF TWO LITTERMATE PIGS BOTH HEREDITY AND ENVIRONMENT MAY BE RESPONSIBLE FOR DIFFERENCES BETWEEN INDIVIDUALS. (COURTESY OF THE UNIVERSITY OF MISSOURI.)



mains the same, barring mutations, for the remainder of its life. Hereditary variations are due to many kinds of gene action, which are both of an additive and a nonadditive nature. Thus, the phenotype of an individual is affected not only by the way each individual gene expresses itself, but also by its expression when in combination with others.

The exact genotype of a particular individual within a herd is never known with certainty, with the possible exception of a few traits influenced by a single pair of genes. If we had some method of accurately determining the genotype of an individual for all of its genes, animal breeding would be much simpler. This is impossible at the present time, but we can get an estimate of the kinds and combinations of genes an individual in a population possesses by observing or measuring the individual's own phenotype as well as the phenotypes of its ancestors, its progeny, and its collateral relatives, that is, those that are neither its ancestors nor its descendants. This will be discussed more fully in the chapter on selection.

ENVIRONMENT

Variations due to environment are also of great importance in animal breeding. The environmental portion of the variance is called the *environmental variance* and may be denoted by the symbol (σ_E^2). Environment includes all such factors as disease, nutrient supply, temperature effects, accidents, and so forth that the individual encounters from the time of conception until death.

JOINT ACTION (INTERACTION) OF HEREDITY AND ENVIRONMENT

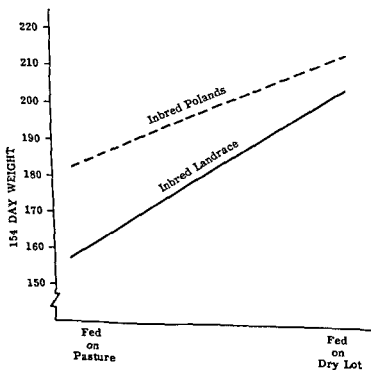
The interaction of heredity and environment means that animals of a certain genotype may perform more satisfactorily in one environment than they do in another. In other words, one environment permits the

expression of the genetic characters in a breed or strain, while another does not. This is illustrated by the data presented in Figure 24. These data show that the inbred Poland pigs were 23 pounds heavier at 154 days of age than were the inbred Landrace pigs when both were fed the same ration on pasture, but that the difference was only 10 pounds when they were fed in dry lot. Thus, the Landrace pigs grew faster in comparison to the Poland pigs in dry lot than on pasture; which is another way of saying that the dry-lot conditions permitted the genes involved to achieve more complete expression. This seems reasonable, since the Landrace breed was originally developed under dry-lot conditions, whereas the Polands were developed to a greater extent on pasture.

Another example of the interaction of heredity and environment involves the performance of the Brahmans and their crosses in the southern and southwestern portion of the United States. Since they are more resistant than the British breeds to certain diseases, parasites, and high temperatures of that region, they perform more satisfactorily under those conditions. When compared with the British breeds under more desirable environmental conditions in the Midwest, however, they may not enjoy this advantage.

Still another example of the interaction of heredity and environment is the disease in humans and animals known as diabetes. This disease is

FIGURE 24 EXAMPLE OF GENETIC \times ENVIRONMENTAL INTERACTION IN INBRED LINES OF SWINE CONCERNING 154 DAY WEIGHTS WHEN FED ON PASTURE AND ON DRY LOT.



characterized by the inability to metabolize glucose properly, so that the level of glucose in the blood stream becomes high, and glucose is excreted with the urine.¹ This disease was almost always fatal to humans before insulin was discovered as a means of treatment. Insulin is produced by the pancreatic gland and when released into the blood stream it causes a reduction in the blood-sugar level. The predisposition to develop diabetes seems to be inherited, but the disease may not develop unless the insulin-producing mechanism of the pancreas is overtaxed over a long period of time by the consumption of excess amounts of carbohydrates.⁴ Under such conditions, insulin production becomes inadequate and diabetes develops. Thus, the right kind of internal environment is necessary to cause this inherited condition to become manifest.

Breeders should be interested in knowing if genetic-environmental interactions are important, and such knowledge should help answer the question of whether or not selection of animals for improvement in one set of conditions would also result in genetic improvement in another. Studies with dairy cattle indicate that the progeny of dairy sires rank similarly when their daughters are fed at different levels. In experiments with mice, however, evidence for genetic-environmental interactions was obtained.³ In these experiments, two strains of mice derived from a single foundation stock were selected exactly in the same manner for weight at six weeks of age. One of these strains was fed *ad lib.*, while the other was restricted to about 75 per cent of the normal food intake between the ages of three and six weeks. The weight at six weeks increased under selection pressure in both strains. Exchanges of feeding levels were made for the two strains after five, seven, and eight generations of selection. The results showed that the improvement for rapid growth on a high plane of nutrition carried with it no improvement for rapid growth on a low plane. On the other hand, improvement of the genotype for rapid growth on a low plane of nutrition did carry with it a considerable improvement for growth on a high plane of nutrition.

In the past, the interaction of heredity and environment in causing variations was not considered to be very important, but now geneticists realize that this factor must be recognized. Genetic-environmental interactions are now being studied by some of the experiment stations, and more complete information should be available in the future. In the meantime, we must assume that interaction is important and must try to produce and select breeding stock under the same conditions in which the offspring will be produced.

IMPORTANCE OF HEREDITY AND ENVIRONMENT

Frequently discussed has been the question whether heredity or environment is the more important in the expression of economic traits.



FIGURE 25 THESE PUREBRED CALVES ARE THIN BECAUSE THEY HAVE BEEN ON A MAINTENANCE RATION OF ROUGHAGE DURING THE WINTER MONTHS THEY HAVE THE INHERITANCE NECESSARY TO MAKE RAPID AND EFFICIENT GAINS AND GOOD CARCASSES IF THEY ARE GIVEN THE RIGHT ENVIRONMENT TO GROW AND FATTEN FOR THE MARKET

Such a discussion here would be of little value, because it is now recognized that both are of very great importance. The best possible inheritance will not result in a superior herd or flock unless the proper environment is also supplied so that the animals can attain the limit set by their inheritance. Half-starved and neglected purebreds are truly a disappointment to livestock men in their appearance as well as in their performance. Nevertheless the best possible environment will not develop a superior herd or flock unless the proper inheritance is also present in the animals. The answer to a question illustrates these statements. Why do not dairymen use beef cows for milk production purposes, and why do not racing enthusiasts include draft animals in their racing strings? The answer is, obviously, that the best possible feed, training, or care cannot make a record breaking milk producer out of a beef cow or a Kentucky Derby winner out of a draft horse. In these extreme examples it can readily be seen that the limit to performance is set by the animal's own heredity, and the best possible environment will not cause that individual to exceed its own genetic potential. At least this does not seem possible, unless we can determine the physiological limitations set by inheritance and can alter these by the use of hormones and other chemicals.

To make the most possible use of good inheritance, we must select breeding animals which are superior because they possess more desirable genes or combinations of genes. Superiority due to genes is the only thing that is transmitted from the parents to their offspring. Superiority due to environment will not be transmitted by the parents. This superior environment must be provided for the offspring if they are to be the equal of their parents.

Environment has received more attention in the past than heredity, but this is changing and more attention is now being given to both. The proper environment is of great importance from the economic standpoint

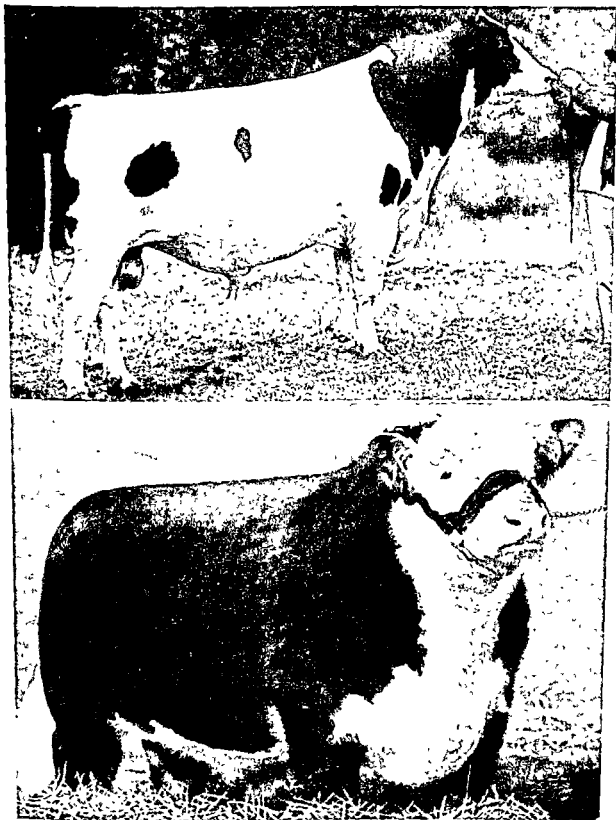


FIGURE 26 A POLLED HEREFORD AND A HOLSTEIN-FRIESIAN BULL. BOTH WERE GRAND CHAMPIONS OF THEIR BREED. ONE IS BRED FOR MEAT AND THE OTHER FOR MILK. THE BEST POSSIBLE ENVIRONMENT WILL NOT ALLOW THEM TO COMPETE SUCCESSIVELY FOR THE PURPOSE EACH IS SELECTED FOR. (COURTESY OF THE AMERICAN POLLED HEREFORD ASSOCIATION AND THE HOLSTEIN-FRIESIAN ASSOCIATION OF AMERICA.)

In addition, it is becoming more and more obvious that animals must be kept in the kind of environment which allows them to show that they possess desirable inheritance for a particular trait. An extreme example here would be the selection of individuals for increased disease resistance. Individual animals must be exposed to the disease in question to determine which of them are resistant. Likewise, the controlled feeding of a boar to reduce his backfat will not also induce less backfat in his offspring if they are full fed a good ration to the usual market weight. A better estimate of the genotype of a boar for backfat thickness will be obtained by feeding him the same ration, and in the same way, that his offspring will be fed.

Breeders often mistake environmental effects for genetic effects when comparing livestock on different farms. The environment can be so different on two farms that the genetically superior animal may look inferior if he has been cared for improperly and so has not had the opportunity to show his full potential. For this reason, it is best to compare the performances of individuals within the same herd where they have been fed and handled in the same manner and not those of individuals in two different herds where the environment might be quite different. Many swine testing stations have been developed so that environment can be more nearly standardized for all animals at a central testing station. This is not the complete answer, however, because the pretest environments could have been quite different for various animals and might affect their performance while they are on test.

The importance of controlling environment as much as possible may be illustrated by the following example. All of the phenotypic variation in a trait is due to hereditary (σ_H^2) and to environment (σ_E^2). The portion of the variation due to heredity would be equal to the hereditary variance divided by the total variance, or:

$$\text{Per cent of hereditary variation} = \frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2} \times 100$$

Let us further assume that σ_H^2 is equal to 20 units and σ_E^2 is equal to 20 units. Thus, the percentage of the variance due to heredity would be

$$\frac{20}{20 + 20} \times 100,$$

or 50 per cent. Suppose, however, that we are able to reduce the environmental variation to such an extent that it is only 10 units. In such a case, the portion of the variance due to heredity would be

$$\frac{20}{10 + 20} \times 100,$$

or 67 per cent.

When we correct weaning weights for every calf in a herd to the same age and same sex, as well as to the same age of dam, we are actually reducing the environmental variations between individuals in that herd, and a larger proportion of the remaining variance should be due to heredity. Thus, the superior individuals, after such corrections are made, would be more likely to be genetically superior, because we would increase our accuracy of picking those which possessed the more desirable genes or combinations of genes.

HERITABILITY ESTIMATES

Heritability estimates refer to that portion of the phenotypic variance in a population that is due to heredity. The percentage of heritability subtracted from 100 gives an estimate of the portion of the variance that is due to environment. Lush⁶ has pointed out that heritability estimates are concerned with the differences between individuals or groups of individuals and not with their absolute values. More correctly, then, when we refer to the heritability estimate for a trait we are referring to the portion of the differences for that trait in a population that is due to heredity. To further illustrate this point, let us assume that the heritability of backfat thickness in swine is 50 per cent and that the average of the herd at a weight near 200 pounds is 1.40 inches. This does not mean that 0.70 inches of backfat is due to heredity and the remaining 0.70 inches to environment. It means that, of the differences between individuals in the herd in backfat thickness, approximately 50 per cent are due to heredity and 50 per cent are due to environment.

Lush has also pointed out that heritability may be used in either a narrow or a broad sense. It is important to understand the difference between the two. In the narrow sense, heritability estimates include mostly the additive type of gene action or the average effects which the individual genes have in that population. This is approximately the same as the percentage of genetic progress made in the next generation when superior individuals are selected for parents. Heritability in the broad sense includes all of the effects of the entire heredity of each individual. Heritability in the broad sense includes, in addition to variations due to additive gene action, those which are due to dominance and epistasis. Most methods of estimating heritability include only a little more than the narrow (or additive) portion of the variation, but this varies with the method used to calculate the estimates.

METHODS OF ESTIMATING HERITABILITY

All heritability estimates are based on how closely relatives resemble each other.⁵ From these calculations an attempt is made to estimate the

degree of correlation between the phenotype and the genotype of individuals in a population. It is not the purpose here to discuss in detail the methods of calculating heritability estimates but we shall outline some of the different methods.

A. Identical twins have been used in genetic studies especially in humans to determine the relative influence of heredity and environment on various traits. Many statistical methods for using twins in genetic research have been developed but all of them depend on the ability to distinguish between one-egg and two-egg twins. One egg twins are derived from the same egg and thus have the same genetic makeup. Any differences between such twins should be of an environmental nature. Fraternal twins or two-egg twins develop from two different eggs and should be no more alike genetically than full brothers and full sisters which are not twins. Variations in two-egg twins would be due to both heredity and environment. Therefore a comparison of two-egg and one-egg twins should give an estimate of the relative influence of heredity and environment on a particular trait. The formula used for obtaining estimates of heritability for certain human traits using identical and unidentical twins is ⁸

$$H^2 = \frac{i^r - f^r}{1 - f^r}$$

where H^2 is the percentage share of hereditary determination of the observed intrapair difference in two-egg twins, i^r the intrapair coefficient of correlation of identical (one egg) twin pairs and f that of fraternal (two-egg) twins. Studies of this kind have shown that intrapair differences are much greater in two-egg twins than in one-egg twins in almost every character studied.

More recently identical twins alone have been used in genetic studies in dairy and beef cattle. In these studies the heritability estimates have been calculated from the formula

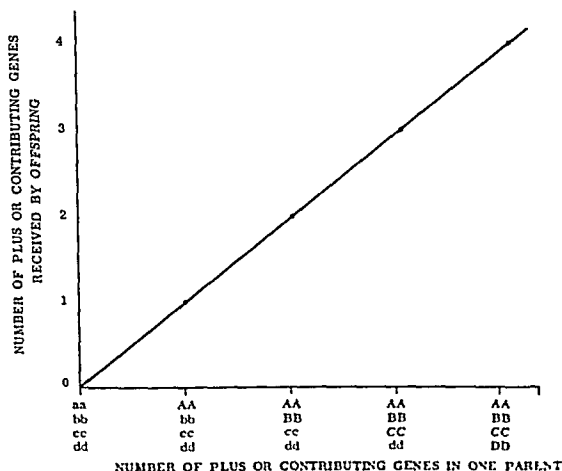
$$H^2 = \frac{(\text{Between pair variance}) - (\text{Within pair variance})}{(\text{Between pair variance}) + (\text{Within pair variance})}$$

Heritability estimates for milk production in dairy cattle derived from records on identical and fraternal twins² range between 70 and 90 per cent as compared to 36 to 50 per cent in studies involving nontwin records from field data. The larger estimates from twin studies may be due to a number of factors. Possibly maternal and contemporary environmental effects may make twin members more alike than nontwins for a particular trait. In addition the genetic variance as estimated from twin data especially from one-egg twins includes that which is due to dominance and epistasis. Little of this kind of genetic variance is included in heritability

estimates obtained from nontwin data. In any event, it appears that heritability estimates from identical twin data are too high and are not a true indication of the progress one would expect to make in selection for a particular trait.

The resemblance between parents and their offspring is also used in calculating heritability estimates in farm animals. This method of calculation can take many forms, depending upon the nature of the records available. One method often used is to determine the intra-sire regression of offspring on the dam. A heritability estimate determined by this method is largely heritability in the narrow sense, which is mostly additive gene action. Still another method often used is to determine the resemblance between sibs. This may be calculated from the intraclass correlations from the analysis of variance. An estimate calculated in this manner is likely to include some of the variations due to epistasis and dominance, as well as to additive gene effects. One convenience of this method is that it is not necessary to know the phenotype of the parents.

FIGURE 27 A THEORETICAL ILLUSTRATION OF HERITABILITY INVOLVING ADDITIVE GENE ACTION. THE OFFSPRING RECEIVE THEIR PLUS OR CONTRIBUTING GENES FROM THE PARENTS. IN THIS EXAMPLE THE HERITABILITY IS 100 PER CENT.



Heritability estimates may also be obtained by calculating the repeatability coefficient for a trait which is the correlation between different records by the same individuals. It gives an estimate of the upper limits of heritability and may be higher than the true heritability, if permanent environmental effects on the individual are important.

VALUE OF HERITABILITY ESTIMATES

Heritability estimates tell something about the amount of progress that might be made in selection for a particular trait. For example, the heritability of rate of gain in beef cattle in the feed lot is about 60 per cent, which means that this percentage of the total variation is due to genes and about 40 per cent is due to environment. Thus, differences in bulls fed on a gain test under similar environmental conditions should be due largely to differences in inheritance, and those making the most rapid gains would be more likely to produce offspring which themselves would make rapid gains. When the heritability of a trait is high, the correlation between the phenotype and the genotype of the individuals, on the average, should also be high, and selection on the basis of the individual's own phenotype should be effective. High heritability estimates also indicate that additive gene action is important for that trait and the mating of the best to the best should produce more desirable offspring.

Quite often, heritability estimates for traits are as low as 10 to 15 per cent or even lower. Litter size in swine is one such trait. A low heritability estimate tells us that there is a low correlation between genotype and phenotype and that if we used superior individuals for that trait for breeding purposes their offspring would not be as superior as when the heritability for a trait was high. To make progress in selection when the heritability of a trait is low, much more attention must be paid to the performance of the collateral relatives and the progeny.

Low heritability estimates also tell us that variations due to additive gene action are probably small. Evidence is also accumulating that when the heritability of a trait is low, nonadditive gene action such as overdominance, dominance, and epistasis may be important. This makes it necessary to use special methods of selection and mating for greater improvement in the herd or flock. These will be discussed more fully in a later chapter.

REPEATABILITY ESTIMATES

Repeatability estimates refer to the expression of the same trait, such as milk production, fleece weight, etc., at different times in the life of the

same individual. Thus, there is no chance for segregation or independent assortment of the genes. On the average, the weaning weight of the calf from a first-calf heifer is about 47 per cent accurate in predicting what her future records will be. Thus, if a cow weans a calf during her first lactation that is 100 pounds heavier than the average of all the heifers of her age in the herd, the cow should wean calves that average 47 pounds above the average of that group in later years.

Another definition of repeatability estimates is that they are the fraction of differences between single records of individuals that are likely to occur in future records of those same two individuals. For example, the repeatability of litter-size at weaning in swine is about 16 per cent. If one gilt weans ten pigs and another six in their first litters, one would expect an average difference in later litters of only 0.64 pigs (16 per cent times four pigs difference).

A knowledge of repeatability estimates for the various traits may be used in selecting for future performance. When the repeatability estimate for a trait is high, culling on the basis of the first record should be effective in improving the over-all record of the herd the next year. In addition, offspring from the superior individuals in the herd should be given preference when selection is made for replacement stock.

Repeatability estimates also tell us something about how to allot animals on a feeding trial. If the repeatability of a trait is high, it becomes increasingly important to divide the offspring of each sire or each dam evenly among the different lots. Otherwise, if the offspring from one parent were in one lot and those of another parent in a second lot, lot differences ascribed to treatment might actually be largely due to hereditary differences. This procedure is of less importance if the repeatability of a trait is low.

Repeatability estimates also give an indication of how many records should be obtained on an individual before it may be culled from the herd or flock. The repeatability of weaning weight in beef cattle is about 47 per cent, whereas it is only about 16 per cent for litter size at weaning in swine. By using the following formula, we can estimate the repeatability of traits where a larger number of records is involved:

$$R = \frac{nr}{1 + (n-1)r}$$

In this formula, R is the repeatability of more than one record, r is the repeatability of one record, and n is the number of records available for purposes of calculation. This formula was used to calculate the repeatability of weaning weight in cattle and litter weight at weaning in swine for one to five records as shown in Table 12. These data indicate that one could cull beef cows for weaning weights of their calves on the basis of a

TABLE 12

REPEATABILITY ESTIMATES FOR WEANING WEIGHT IN BEEF CATTLE
AND LITTER SIZE AT WEANING IN SWINE WITH ONE TO
FIVE RECORDS

No. of Records	Repeatability in per cent	
	Weaning Weights in Beef Cattle	Litter Size at Weaning in Swine
1	47	16
2	64	28
3	73	36
4	78	43
5	81	49

single record with almost as much confidence as one could cull sows for litter size at weaning on the basis of five records.

Lifetime averages which show the ability of certain individuals to repeat a high level of performance over a long period of time are very important in animal breeding. These records should be as accurate as possible and should be corrected for certain environmental factors before individuals in a herd are compared. Lush⁷ has suggested the following formula for adjusting the records of cows with different numbers of records to the same basis, and he has called this the *probable producing ability* of an individual:

$$\text{Probable producing ability} = \text{Herd average} + \frac{nr}{1 + (n-1)r} \times \begin{matrix} \text{Her own average} \\ \text{minus the herd} \\ \text{average} \end{matrix}$$

Such a record could be used for culling females from a herd where there is considerable variation in ages and numbers of records.

Lifetime averages are of value in selecting for traits in which the repeatability is low, but their value is decreased by the fact that the generation interval is increased and progress per year may be slow. A consistently high performance over a period of many years is a good indication that an animal possesses desirable genes for several traits. Whenever possible, both male and female replacement stock should be retained from such dams. Such a record would be useful in selecting for increased vigor, constitution, and longevity, which may be indicative of freedom from recessive or partially dominant genes with detrimental effects.

In conclusion, it has been pointed out in this chapter how variations in individuals are the raw material with which the animal breeder must work. It was further pointed out that the genetic variations within a herd or flock more truly are the raw material with which the breeder must

work to make progress through the application of breeding methods. Methods used to measure the genetic portion of the variations in economic traits were also discussed. A more detailed discussion of how this information may be used for the improvement of each species of farm animals will follow in later chapters.

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Questions and Problems

- 1 Explain why variation is the raw material with which the animal breeder must work
- 2 Which is the more important, inheritance or environment?
- ✓ 3 What are the causes of phenotypic variation in farm animals?
- ✓ 4 Explain the meaning of genetic-environmental interactions and why they might be of importance to the animal breeder
- ✓ 5 Define the term *heritability estimate* and explain the difference between heritability in the narrow sense and in the broad sense
- 6 Of what use to the animal breeder is a knowledge of heritability estimates?
7. Discuss some of the ways that the heritability of a trait may be measured in farm animals

- 8 What is the meaning of a repeatability estimate and how may a knowledge of this be used for livestock improvement?
- 9 Why are lifetime averages of great importance to the animal breeder? What are their disadvantages?
- 10 A farmer has a herd of swine which on the average weigh 195 pounds at six months of age. He selects for breeding purposes gilts which average 205 pounds and boars which average 225 pounds at six months of age. The offspring produced have an average six month weight of 194 pounds. What is the apparent heritability of six month weight in swine in this example?
- 11 A simple way to estimate heritability is to divide the dams mated to a sire into two groups namely a high producing group and a low producing group. The daughters of these two groups of dams are then tested for production. A dairy sire (X) is mated to two groups of cows. The high producing group averages 650 pounds of butterfat and the low producing group averages 500 pounds. The daughters of these two groups of dams average 585 and 570 pounds respectively. What is the apparent heritability of butter fat production in this example?
- 12 Assume that the repeatability of weaning weight in beef cows is 47 per cent when based on one record, 64 per cent when based on two records, and 73 per cent when based on three records. In a herd which averages 400 pounds in the calves at weaning, which of the three cows would you rather retain for breeding purposes: cow A with one calf weaned weighing 490 pounds; cow B with three calves weaned weighing an average of 460 pounds; or cow C with two calves weaned weighing an average of 490 pounds?

14

Principles of Selection ✓

SELECTION MAY BE DEFINED AS A PROCESS in which certain individuals in a population are preferred to others for the production of the next generation. Selection is of two general kinds, natural, or that due to natural forces, and artificial, or that due to the efforts of man.

No new genes are created by selection. Under selection pressure there is a tendency for the frequency of the undesirable genes to be reduced whereas the frequency of the more desirable ones is increased. Thus, the main genetic effect of selection is to change gene frequencies, although there may be a tendency also for an increase in homozygosity of the desirable genes in the population as progress is made in selection.

NATURAL SELECTION

In nature, the main force responsible for selection is the survival of the fittest in a particular environment. Natural selection is of interest because of its apparent effectiveness and because of the principles involved.

Natural selection may be illustrated by considering the ecology of some of our wild animal species. Murie³ studied the relationship between wolves in Mt. McKinley National Park in Alaska and other species of animals, especially the Dall or mountain sheep. Apparently, the wolves chase many sheep before they find one they can catch. Most of those killed by the wolves were the weaker animals, and included those which were either very young or very old. Thus, there was a tendency for nature to select against the weaker ones, and only the stronger survived to reproduce the species.

Some of the most interesting cases of natural selection are those involving man himself. All races of man that now exist belong to the same species, because they are interfertile, or have been in all instances where matings have been made between them. All races of man now in existence

had a common origin, and at one time probably all men had the same kind of skin pigmentation—which kind we have no sure way of knowing. As the number of generations of man increased, mutations occurred in the genes affecting pigmentation of the skin, causing genetic variations in this trait over a range from light to dark or black. Man began to migrate into the various parts of the world and lived under a wide variety of climatic conditions of temperature and sunshine. In Africa, it is supposed, the dark skinned individuals survived in larger numbers and reproduced their kind, because they were better able to cope with environmental conditions in that particular region than were individuals with a lighter skin. Likewise, in the northern regions of Europe men with white skins survived in a greater proportion, because they were better adapted to that environment of less intense sunlight and lower temperatures. But what of the Eskimos who lived in the polar regions of the North? They are also dark skinned. Does this theory fit them? The most probable answer to this question is that the Eskimos are more recent migrants from Asia to the polar region, and compared to the Negro in Africa and the whites in Europe, they have not lived so long in that region.

Recently, evidence has been obtained that there may be a differential selection for survival among humans for the A, B, and O blood groups¹. It has been found that members of blood group A have more gastric carcinoma (cancer) than other types and that members of type O have more peptic ulcers. This would suggest that natural selection is going on at the present time among these different blood groups, and the frequency of the A and O genes might be gradually decreasing unless, of course, there are other factors that have opposite effects and have brought the gene frequencies into equilibrium.

Natural selection is a very complicated process, and many factors determine the proportion of individuals that will reproduce. Among these factors are differences in mortality of the individuals in the population, especially early in life, differences in the duration of the period of sexual activity, the degree of sexual activity itself, and differences in degrees of fertility of individuals in the population.

It is interesting to note that in the wild state, and even in domesticated animals to a certain extent, there is a tendency toward an elimination of the defective or detrimental genes that have arisen through mutations, through the survival of the fittest.

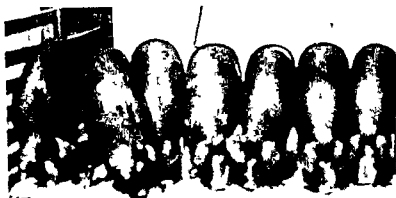
ARTIFICIAL SELECTION

Artificial selection is that which is practiced by man. Thereby, man determines to a great extent which animals will be used to produce the

next generation of offspring. Even here, natural selection seems to have a part. Some research workers have divided selection in farm animals into two kinds, one known as automatic and the other as deliberate selection.² Litter size in swine may be used as an illustration of the meaning of these two terms. Here, automatic selection would result from differences in litter size even if parents were chosen entirely at random from all individuals available at sexual maturity. Under these conditions, there would be twice as much chance of saving offspring for breeding purposes from a litter of eight than from a litter of four. Automatic selection here differs from natural selection only to the extent that the size of the litter in which an individual is reared influences the natural selective advantage of the individual for other traits. Deliberate selection, in this example, is the term applied to selection in swine for litter size above and beyond that which was automatic. In one study by Dickerson and co-workers involving selection in swine² most of the selection for litter size at birth was automatic and very little was deliberate; the opportunity for deliberate selection among pigs was utilized more fully for growth rate, however.

Definite differences between breeds and types of farm animals within a species is proof that artificial selection has been effective in many instances. This is true, not only from the standpoint of color patterns which exist in the various breeds, but also from the standpoint of differences in performance that involve certain quantitative traits. For instance, in dairy cattle there are definite breed differences in the amount of milk produced and in butterfat percentage of the milk.

FIGURE 28 ABOVE, FAT HOGS IN 1912, AND BELOW FAT HOGS IN MORE RECENT TIMES. CHANGES IN CONSUMER DEMANDS FOR MORE LEAN AND LESS FAT TOGETHER WITH SELECTION PRESSURE FOR THE MEAT-TYPE HOG HAS WROUGHT THIS CHANGE IN TYPE.



SYSTEMS OF SELECTION FOR DIFFERENT KINDS OF GENE ACTION

The different kinds of gene action that affect economic traits in farm animals were discussed in Chapters 5 and 6. It was pointed out that, in general, quantitative traits, such as milk production, rate of gain, and backfat thickness, are probably affected by many pairs of genes, each pair of which has small effects on a particular trait. Nevertheless, there is also evidence that single pairs of genes can have large effects on economic traits, especially such genes as the one for dwarfism in beef cattle. It is important for the breeder to know how to select for different kinds of gene action.

SELECTION FOR A DOMINANT GENE

In practice, we are very likely to be selecting for a dominant gene because traits determined by such a gene are usually desirable. Those that possess a dominant gene will show it but the problem here is one of distinguishing between the homozygous dominant and the heterozygous individuals. The heterozygous individuals must be identified before they can be eliminated.

SELECTION AGAINST A DOMINANT GENE

Selection against a dominant gene is relatively easy, providing the penetrance of the gene is 100 per cent and it does not vary in its expression. Since each animal possessing a dominant trait should show this in its phenotype, eliminating the gene merely means that all animals showing the trait should be discarded. Whether or not this can be done at once, of course, depends upon the number of animals possessing the trait and whether one can afford to discard all of them at one time.

If the penetrance of the gene is low and the genes are variable in their expression, selection against a dominant gene would be much less effective. Selection for such a trait could not be based upon the individual's phenotype alone, but attention to the phenotype of the ancestors, progeny, and collateral relatives would also be necessary if selection were to be successful.



FIGURE 29 A BLACK ANGUS COW AND HER RED ANGUS CALF
THIS IS A RECESSIVE TRAIT AND BOTH PARENTS HAD TO BE CARRIERS OF THE RED GENE. THIS IS AN EXAMPLE OF A TRAIT IN WHICH RED INDIVIDUALS HAVE BEEN CULLED FOR MANY GENERATIONS BUT THE RECESSIVE GENE HAS NOT BEEN ELIMINATED FROM THE BREED.

show the recessive trait. A good example of such selection would be for the horned gene in cattle. To produce all horned cattle, one merely has to obtain horned breeding stock and mate them together. The only time polled individuals would be produced from such a mating is when a mutation from the horned to the polled gene occurs. This is so infrequent that it is seldom observed in an average size herd.

SELECTION AGAINST A RECESSIVE GENE

Selection against a recessive gene is quite difficult, because it becomes necessary to identify the heterozygote, either by some phenotypic method, which seldom can be done, or by a breeding test. Merely discarding the homozygous recessive will not completely eliminate a recessive gene, although it may lower the frequency of its occurrence in a population. The latter is true, of course, providing that the heterozygous individual is not favored in selection.

The following is a formula for determining the frequency of a gene in a population in which all of the homozygous recessive individuals are discarded

$$F_n = \frac{F_0}{1 + (N \times F_0)}$$

where

F_n is the frequency of the recessive gene after all homozygous recessive individuals have been discarded for n generations

F_0 is the original frequency of the recessive gene before the homozygous recessive individuals were discarded

N is the number of generations of selection against the homozygous recessive individuals

For example let us assume that the frequency of a recessive gene in a population is 0.10. What would be the frequency of this recessive gene (F_n) after four generations of selection in which all homozygous individuals were discarded? The answer to this problem is

$$F_n = \frac{0.10}{1 + 4(0.10)} = \frac{0.10}{1.40} = 0.071$$

Data presented in Figure 30 were calculated by using the above formula on a theoretical population in which the original frequency of the recessive gene was 0.50. Complete selection was then practiced against the homozygous recessive individuals for 20 generations. It will be noted that progress in selection against the recessive gene was very rapid at first with a sharp decline in the frequency of the recessive gene during the first few generations of selection. But as selection continued, the rate at which the frequency of the recessive gene was lowered became less and less. This is what may be expected in a large population where selection against a recessive gene is based on phenotype alone. Actually, the population will probably never be freed of the gene unless the heterozygous individuals are also identified and discarded along with those which are homozygous recessive.

A number of breeding tests may be used to identify heterozygotes. One homozygous recessive offspring of course, proves both parents to be carriers of the recessive gene. It is possible according to the law of chance, for individuals that are carriers of a recessive gene to produce several offspring none of which are homozygous recessive. Certain mathematical limits have to be set in such cases when individuals are being tested to determine if they are homozygous dominant or heterozygous.

One of the simplest methods to use in testing for carriers of a recessive gene is to test-cross to the homozygous recessive individuals. This test

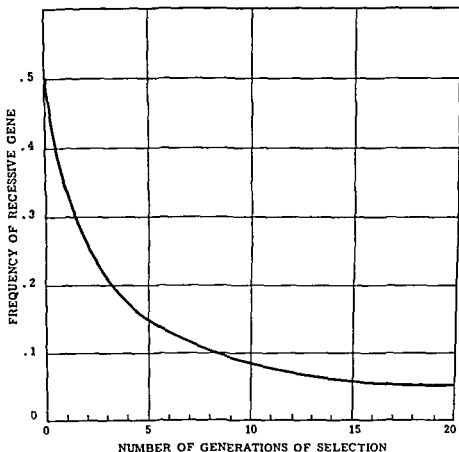


FIGURE 80 SHOWING THE DECREASE IN THE FREQUENCY OF THE RECESSIVE GENE IN A POPULATION WHEN ALL HOMOZYGOUS RECESSIVE INDIVIDUALS ARE DISCARDED AND THE HETEROZYGOTE IS NOT FAVORED IN SELECTION.

cross, as it is often called in genetics, depends upon the survival and fertility of the homozygous recessive individuals. As a result, it sometimes cannot be used. In cattle, for instance, horned individuals are usually available for testing purposes, but dwarfs seldom survive to breeding age and usually cannot be used for testing purposes.

A polled bull may be tested to determine whether he is a carrier of the horned gene by mating him to horned cows. But the question here is, how many horned cows must he be mated to before we can conclude that he is probably homozygous for the polled gene? We can go back to the chapter on probabilities and use one of the rules given there for answering this question. The probability that any one calf will be polled from a mating of a heterozygous polled bull to horned cows is $\frac{1}{2}$. The probability of two calves being polled from a mating of such parents is the product of the separate probabilities, or $\frac{1}{2}$ times $\frac{1}{2}$, or $\frac{1}{4}$. The number of matings may be increased until we find that the probability of all polled calves from the mating of a heterozygous polled bull to five horned cows is $\frac{1}{32}$. This is a probability of $\frac{1}{32}$, or about 3.1 chances in 100 that all polled calves will be produced. This leads to the conclusion that, if a polled bull of unknown genotype is mated to five horned cows without

TABLE 13

NUMBERS AND KINDS OF MATINGS REQUIRED TO TEST A MALE TO DETERMINE THAT HE IS NOT A CARRIER OF A RECESSIVE GENE

Kinds of Females	Probability Test* Females are Carriers	No of Matings Required Without the Production of Homozygous Recessive Offspring at Odds of	
		95/100	99/100
1 Homozygous recessive	1 00	5	7
2 Known heterozygotes**	1 00	11	16
3 Phenotype normal and genotype unknown but both sire and dam known heterozygous	0 67	17	26
4 Phenotype normal and at least one parent known heterozygous	0 50	24	35
5 Test bull mated to own daughters	0 50	24	35

* Females in groups 3 4 and 5 must be a random sample with no single female counted twice

** Known heterozygotes may be of two types—those that have produced at least one homozygous recessive offspring or those having one parent known to be homozygous recessive

producing a horned calf, he is not a carrier of the horned gene. We would expect to be right at odds of 97 out of 100. Six such matings without a horned calf being produced would increase the odds we are right to 98 times out of 100. The same probabilities would hold if he were mated to five different horned cows or to the same horned cow until five calves were produced.

Actually, in such a breeding test, we can never be absolutely certain that a bull is homozygous for the polled gene, but our confidence should increase with each polled calf he sires out of horned cows. In many instances, the laws of probability may be used to estimate the probability that a particular individual in the herd is homozygous dominant, especially a male, without running a special test. Records should be checked to make certain that enough matings of the required kind have not already been made which would give an indication of probable genotype of the animal in question.

In those species such as swine where multiple births occur, it is much simpler to test for heterozygosity for a recessive gene than it is in cattle, where a single birth usually occurs. The mating of a male of unknown genotype to a sow that is homozygous recessive for a particular gene will

often prove the boar with one litter. This is especially true where litter size includes five or more pigs.

In farm animals such as cattle where single births are the rule, it becomes more difficult to test females as carriers of a recessive gene by a breeding test. Five or more matings would have to be made to a bull of the homozygous recessive genotype without the production of a single homozygous recessive offspring before we would have confidence that she was homozygous dominant. Thus, it would require a lifetime of planned testing although attention to the records of her offspring and a complete study of the records of her ancestors and sibs should be helpful in arriving at an estimate of her genotype. In swine, where large litters are produced, it is often practical to test females to determine whether they are carriers of a recessive gene.

Sometimes it is not possible to backcross to the homozygous recessive individuals, because they may fail to survive to breeding age, or may be infertile. In such cases, other methods of breeding must be used.

Four methods may be used to test for carriers of a recessive gene such as dwarfism where homozygous recessive individuals are not available for the backcross test. These are as follows:

(1) A male to be tested can be mated to females known to be heterozygous because they have produced a dwarf calf. If a bull is mated to 11 known carrier cows and all of the calves are normal, the chances are about 95 out of 100 that the bull is homozygous normal. Sixteen such matings without the production of a dwarf calf would increase the chances that he is homozygous normal to about 99 out of 100.

(2) A bull may be tested by mating him to cows of unknown genetic make up but whose sires and dams were known to be heterozygous for the recessive gene. All normal calves from mating such a bull to 17 different cows would indicate that he is homozygous normal at odds of 95 out of 100, and all normal calves out of 26 different cows of this kind would indicate that he was homozygous normal at odds of 99 out of 100.

(3) A third way of testing a bull is to mate him to cows which are known to be from at least one heterozygous parent. Under these conditions, 24 normal calves prove a bull homozygous normal at odds of 95 out of 100, and 35 normal calves at odds of 99 out of 100.

(4) A fourth type of test that can be made is to mate a bull to his own daughters. When a bull is mated to 24 of his own daughters and no dwarf calves are produced the chances are 95 out of 100 that he is homozygous normal for that gene. Thirty five normal appearing calves out of his own daughters will prove him homozygous normal at a 99 out of 100 level of probability. Obviously, one disadvantage of such a method of testing is that inbreeding may result in reduced vigor of the calves. Furthermore, the bull will be several years of age before he has that many daughters to which he can be mated. On the other hand, such a method of testing

helps uncover all recessive genes the bull may be carrying in addition to those which cause dwarfism

It is apparent that there are certain advantages and disadvantages for each of the breeding tests described. It should be emphasized also that in methods 2, 3, and 4 cows used for mating purposes should be a random sample and that no cow should be used twice for testing the same bull. Likewise it might be possible to use a combination of several of the above kinds of females for testing purposes.

SELECTION FOR MULTIPLE ALLELES

It is not known for certain if one or more series of multiple alleles affect economic traits in farm animals although they are known to affect traits such as coat color and blood types in cattle. If a series of multiple alleles such as A^1 , A^2 , and A^3 did exist it is possible that one might have more favorable effects on a trait than do the other two. Genetic improvement would come about by culling the less desirable animals for that particular trait and mating the best to the best. By doing this the frequency of the desirable allele should be increased in the population.

SELECTION FOR EPISTASIS

As pointed out earlier epistasis is the interaction between genes which are not alleles and this interaction may be of several different kinds. The action may be either complementary or inhibitory but we do not know for certain in what manner the genes may act as far as their influence on the important economic traits in farm animals are concerned. We do have evidence however that epistasis may be of considerable importance in determining the performance of farm animals.

If epistatic action is of a complementary nature and it probably is in many cases advantage could be taken of this kind of gene action by forming inbred lines and then testing them in crosses to find those that are superior in this respect. The formation of inbred lines however is a rather expensive procedure and in farm animals probably enough good lines could not be formed to locate those with the best combining ability as has been done with inbred lines of corn. This is more likely to be done with swine than in any other class of farm animals since swine are more prolific and the interval between generations is not so long as in dairy and beef cattle.

The formation of many inbred lines within a breed testing these in crosses and then combining those with the most desirable combining ability followed by inbreeding once more should be helpful in developing superior inbred lines if epistasis is of importance. This is probably too time-consuming and expensive to be of much practical value. Inbred

lines could also be formed from breed crosses, as has been done in many cases,⁴ and perhaps superior breeds or lines could be developed by such methods. It is doubtful, however, if one could ever fix all of the favorable epistatic effects in a single breed, regardless of the efforts applied to this end.

SELECTION FOR OVERDOMINANCE

Overdominance is the interaction between genes that are alleles and is a theoretical type of gene action involving many different pairs of genes with small individual effects. Using one pair of alleles as an example, we would say that the heterozygous individual, a^1a^2 , would be superior to either homozygote, a^1a^1 , or a^2a^2 .

As was pointed out earlier, it is never possible to make the heterozygous individuals breed true, because the mating of such individuals in the above example would result in the segregation into the three different genotypes in a 1:2:1 ratio. A good example of such a case is coat color in Shorthorn cattle. Roan cattle are heterozygous (RW) and possess one gene for red and one for white coat color. This is a blending type of inheritance where neither gene is dominant to the other. The mating of roan cattle results in the production of 1 red:2 roan:1 white. In spite of the fact that roan individuals do not breed true, it is possible to make matings in such a way that roan individuals may always be produced. This can be done by merely mating red (RR) with white (WW) individuals. Since the genotype may be distinguished by the phenotype, such matings can be made rather easily.

It is not possible to determine from their phenotype the genotype of individuals for certain economic traits. This is especially true where many pairs of genes with small effects may be involved. We do know, however, from a theoretical standpoint, that if the heterozygous individual does not breed true, we cannot hope to take advantage of overdominance by combining these genes into a single superior breed. We know also that, in order to always produce heterozygous individuals, we must cross lines or strains that are homozygous for the several pairs of genes that give the overdominant type of gene action. This may be illustrated in the following example:

$$\begin{array}{ccc}
 a^1a^1b^2b^2c^1c^1d^1d^1 & \times & a^2a^2b^1b^1c^2c^2d^2d^2 \\
 \text{Inbred line one} & & \text{Inbred line two} \\
 & & a^1a^2b^1b^2c^1c^2d^1d^2 \\
 & & \text{Linecross offspring}
 \end{array}$$

Even though we cannot tell the genotypes of inbred line one and inbred line two from their phenotypes, we get some idea of how they complement each other by the performance of their crossbred, or F_1 , progeny.

This will allow us to practice a kind of selection known as *reciprocal recurrent selection*, which, theoretically, at least, should be helpful in improving the nicking or combining ability of two inbred lines

The procedure in practicing this kind of selection is to test many inbred lines in crosses to identify those that produce the superior crossbred offspring. Then two or more of these lines could be selected for superior combining ability by making reciprocal crosses between them, that is, by crossing boars of one line with sows of the other line, and vice versa, so that boars and sows of each line could demonstrate their crossing ability based on the performance of their crossbred progeny. The boars and sows from each line that demonstrated their ability to produce superior crossbred offspring could then be used to produce the pure line in the next generation. Several generations of such selection might improve the overall crossing or nicking ability of the two lines.

It can be seen, however, that the system of reciprocal recurrent selection is time consuming and costly. Its effectiveness has not yet been thoroughly tested in farm animals, and its effectiveness may not be fully determined for a number of years. In the meantime, advantage may be taken of this kind of gene action and that of epistasis by crossing different breeds to produce crossbred offspring.

SELECTION FOR ADDITIVE GENE ACTION

It has already been pointed out that additive gene action is thought to be of considerable importance in the expression of quantitative traits of great economic importance such as rate of gain, milk production, carcass quality, and others. When this kind of gene action is important, selection merely becomes a matter of finding those individuals which are superior for the trait and then mating the best to the best, year after year. If this is done eventually most of the contributing genes could be combined into one breed or one herd although this depends upon efforts to make selection as effective as possible.

References

Questions and Problems

- 1 What is selection?
- 2 What is the main genetic effect of selection?
- 3 Distinguish between artificial and natural selection
- 4 Outline methods of selection to follow to eliminate a dominant gene from a herd, a recessive gene
- 5 What methods of selection should be followed in improving traits affected largely by nonadditive gene action such as epistasis and overdominance, for traits influenced largely by additive gene action?
- 6 Assume that the frequency of a recessive gene in a large population of cattle is 0.05. All homozygous recessive individuals are discarded and not used for breeding purposes. What would be the probable frequency of the recessive gene after six generations of selection?
- 7 In question 6, what would be the frequency of the dominant gene before selection was practiced and again after six generations of selection against the recessive gene?
- 8 Assume that the frequency of the recessive gene in question 6 actually increased, instead of decreasing, after six generations of selection against the homozygous recessive individuals. What would be the possible explanation?

15

Selection of Superior ✓ Breeding Stock

ANY PROGRESS ANIMAL BREEDERS MAY

hope to make through the application of breeding and selection methods will depend upon their ability to recognize those animals which possess superior inheritance. These superior animals must be mated together for the production of superior offspring. The only way we have at present of estimating the kind of genes an animal possesses is through their expression in the phenotype of the individual and/or his relatives. Figure 31 illustrates the kinds of relatives an individual has, on which selection may be based.

SELECTION ON THE BASIS OF INDIVIDUALITY

Selection on the basis of individuality means that animals are kept for breeding purposes on the basis of their own phenotype. Selection may be made for several traits such as coat color, conformation, performance, or carcass quality. In the past the most emphasis in selection probably has been based on coat color and conformation, although performance and carcass quality have received more attention in recent years.

Most of the breeds of livestock are characterized by a particular coat color or color pattern and this is one of the requirements for entry into the registry associations. Selection for coat color has been practiced because of its aesthetic value rather than its possible correlation with other, important economic traits.

Attempts to relate variations of coat color to performance within a breed have not met with success from the experimental standpoint, although many livestock men feel that there is a relationship. The strong belief of horse breeders that there is a strong relationship between color and temperament seems to be refuted by actual experimental data.⁴ Nev

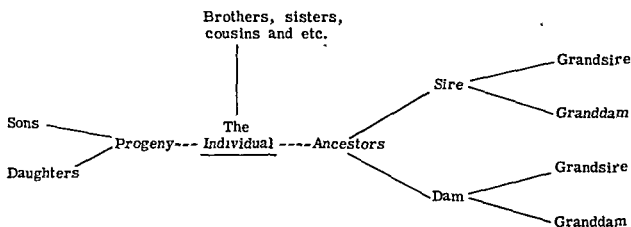


FIGURE 31 DIFFERENT KINDS OF RELATIVES OF AN INDIVIDUAL UPON WHICH SELECTION MAY BE BASED.

ertheless, there is evidence that animals of some colors may be better able to cope with certain environmental conditions, such as high temperatures and intense sunlight in some regions of the tropics or in the South and the Southwestern portions of the United States.

As was pointed out in Chapter 11, coat color in some instances is closely related to lethal and undesirable genes in farm animals. In addition, many cases in animals of other species, such as the mouse, dog, cat, mink, and fox, also show such relationships. How important this relationship might be in the efficiency of livestock production will have to await further experimental results.

Certain coat colors are the trademark of the various breeds of livestock. This is probably because this is a characteristic easily recognized, even by the novice. Whether or not animals of one color are superior to those of another may not be important. The important point is that the breeder must conform to the breed requirements for this trait, or he will not be in the purebred business for long.

(A) Type and conformation have been used as the basis of selection for many years throughout the world. Type may be defined as the ideal of body construction that makes an individual best suited for a particular purpose. This basis of selection has merit in some instances. The conformation of a draft horse is such that he is better suited to pulling heavy loads than he is to racing. On the other hand, the reverse is true of the thoroughbred.

The performance of individuals has also been given some attention in the development of some of our breeds of livestock. For many years thoroughbred horses have been selected for breeding purposes for their speed. Dairy cows have been selected for their ability to give large amounts of milk and butter fat. In beef cattle and swine, however, less attention has been paid to selection for performance and carcass quality until the last few years, except possibly in swine in Denmark.

Increased emphasis is now being placed on selection for performance and carcass quality, because breeders realize that the type or conformation of an individual is not the best indicator of its potential performance or its carcass quality. More exacting measures of these traits must be applied before progress can be made in selection for them.

The correlation between type and carcass quality is greater in some instances than is the correlation between type and performance. We can tell something about the meatiness of hogs by a visual inspection, but this is not reliable. Better methods are backfat probes on live animals, actual weighings and measuring of lean meat in the carcass.

The fact that type and performance are not usually closely related indicates the importance of selecting separately for the important traits in livestock production. If the correlation between type and other traits is low, this indicates that they are inherited independently and that all will be improved only if selection is practiced for each of them.

Individuality for certain traits should always be given some consideration in a selection program. However, it is more important in some instances than in others. It is most important as the basis of selection when the heritability of a trait is high, indicating that the trait is greatly affected by additive gene action. High heritability estimates also suggest that the phenotype strongly reflects the genotype and that the individuals that are superior for a particular trait should also possess the desirable genes for that trait and should transmit them to their offspring.

(2) - The greatest disadvantage of selection on the basis of individuality is that environmental and genetic effects are sometimes difficult to distinguish. Much of the confusion may be avoided by growing or fattening the offspring being compared for possible selection purposes under a standard environment. Even then it is still possible to mistake some genetic effects for environmental effects. This is less likely to happen, however, in the outstanding individuals than in those that have a mediocre record. For instance, a bull calf placed on a performance test may make a poor record because of an injury or because of sickness while on test. But if he makes an outstanding record, we are pretty certain that he possessed the proper genes and in the right combination as well as the proper environment to make the good record. We cannot always be certain, however, whether an individual with a mediocre record would have done better even if adverse environmental factors had not interfered. We can be certain that his record is poor and, culling on this basis, we will also eliminate the genetically poor individuals. This chance is worth taking, even though we may discard some genetically superior individuals occasionally.

Studies of selection on the basis of individuality within inbred lines of swine have shown that selection favored the less inbred litters. This is another way of saying that selection probably favored the more hetero-

Pedigree of Brilliant Miss Royalty 895658 11 - STAR PR 439

Raised 11 consecutive litters all PR qualified.

Av. 11.72 Farrowed

Av. 10.18 Raised

387.4 lbs at 56 days

Transformer's Masterpiece

326965 3 - STAR PR 21

Has 28 dau. with 52 litters.

Av. 11.15 pigs Farrowed,

9.67 pigs Raised,

358.35 lbs. at 56 days

Kasters Queen

707876

Transformer 286723

1 - STAR PR 22

9 dau.: 19 litters

Av. 11.15 Farrowed

9.67 Raised

358.35 lbs at 56 days

Steam Roller 256561

2 - STAR PR 12

17 dau.: 23 litters

Av. 10.8 Farrowed

10 Raised

370.48 lbs. 56 days

Harper's Sue 3rd

639384

Master Roller

277319

Dolls Gal

666442

The Mercury

267327

Cesar's Brilliant

Princess 651608

Century of Earlham 259101

8 tested dau.: 12 PR litters

Av. 11.58 Farrowed

9.75 Raised

372 lbs. at 56 days

Rambler Beauty 630074

3 - STAR PR 28

4-PR litters

Av. 10.75 Farrowed

8 Raised

348.75 at 56 days

Mt. Ararat Brilliant

Beauty 710908

5 - STAR PR 164

5 PR litters

Av. 11.8 pigs Farrowed

9.8 pigs Raised

356.5 lbs. at 56 days.

Litter mate to Mt. Ararat

Bright Beauty

3 - STAR PR 119

Century Hi Roller
Sire of 4 PR boars

Lady Flash

Harpers Hi Hope

Highway Sue

Gardners Roller

Deisy Clan

Wicks Clan

Nebraska Doll 1st

The Clipper Deluxe

Powder Puff

Main Answer

Lady Brilliant 4th

Century Hi Roller

Sire of 4 PR boars

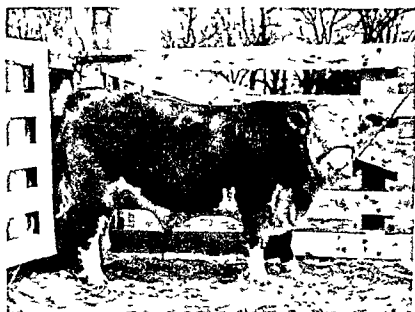
Lady Brilliant 4th

The Clipper Deluxe

Fair Lady

FIGURE 32 PEDIGREE OF BRILLIANT MISS ROYALTY (895658) WHICH INCLUDES INFORMATION ON THE PERFORMANCE OF RELATIVES. A PEDIGREE OF THIS KIND IS OF MUCH MORE USE IN SELECTION THAN ONE CONTAINING ONLY NAMES AND NUMBERS. (COURTESY OF THE AMERICAN HAMPSHIRE SWINE RECORD ASSOCIATION)

FIGURE 33 THIS YOUNG BULL WAS PROVED FREE OF THE DWARF GENE BY THE PROGENY TEST EVEN THOUGH HIS SIRE WAS A KNOWN CARRIER OF THE DWARF GENE.



the individual still has a questionable pedigree and will be condemned by many breeders, either because they are not familiar with the inheritance affecting such a trait or because they are afraid to trust the progeny-test information.

Another disadvantage of pedigree selection is that the individuals in the pedigree, especially the males, may have been selected from a very large group, and the pedigree tells us nothing about the merit of their relatives

Still another disadvantage of pedigree selection is that a pedigree may often become popular because of fashion or fad and not because of the merit of the individuals it contains. The popularity of the pedigree may change in a year or two, and the value of such a pedigree may decrease considerably or may even be discriminated against. If popularity is actually based on merit, there is less danger of a diminution of value in a short period of time.

In using pedigrees for selection purposes, the most weight should be given to the most recent ancestors. This is because the percentage of genes contributed by an individual's ancestors is halved each new generation. Methods of calculating the percentage of genes an individual has in common with some admired ancestor will be presented in a later chapter. Some breeders place much emphasis on some outstanding ancestor three or four generations removed in the pedigree, but such an ancestor contributes a very small percentage of the genes the individual possesses and has very little influence on type and performance, unless linebreeding to that ancestor has been practiced.

An individual's own performance is usually of more value in selection than its pedigree, but the pedigree may be used as an accessory to sway the balance when two animals are very similar in individuality but one

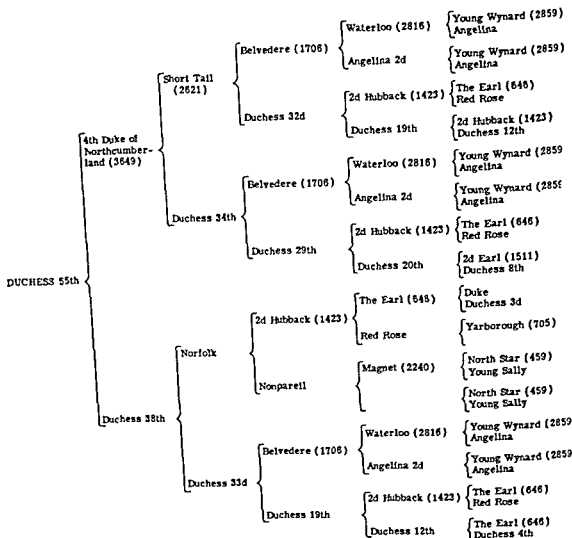


FIGURE 34 PEDIGREE OF DUCHESS 55TH A VERY POPULAR PEDIGREE AT ONE TIME, BUT THE FAMILY LATER LOST POPULARITY BECAUSE OF BARRENNESS IN THE COWS

has a more desirable pedigree than the other. Pedigree information is also quite useful when the animals are selected at a young age and their own type and conformation is not known. Pedigrees are also useful in identifying superior families if good records are kept and are available for study.

SELECTION ON THE BASIS OF COLLATERAL RELATIVES

Collateral relatives are those that are not related directly to an individual, either as ancestors or as their progeny. Thus, they are the individual's brothers, sisters, cousins, uncles, aunts, etc. The more closely they



FIGURE 35 SOME CARCASS CUTS IN LITTERMATE BARROWS, NUMBERS 315 AND 317 LITTERMATES CAN VARY IN SUCH TRAITS BUT GENERALLY ARE MORE ALIKE THAN NONLITTERMATES. (COURTESY OF THE UNIVERSITY OF MISSOURI.)

are related to the individual in question, the more valuable is the information they might supply for selection purposes.

Information on collateral relatives, if complete, gives an idea of the kinds of genes and combinations of genes that the individual is likely to possess. Information of this kind is now being used in meat-hog certification programs, where a barrow and a gilt from each litter may be slaughtered to obtain carcass data. This is done, because otherwise the animal himself has to be slaughtered if information on his own carcass quality is to be obtained. Information on collateral relatives is also used in selecting dairy bulls, since milk production can be measured only in the cows even though the bull transmits genes to his offspring for this trait.

SELECTION ON THE BASIS OF PROGENY TESTS

Selection on this basis means that we estimate the breeding value of an individual through a study of the traits or characteristics of its offspring. In other words, the progeny of different individuals are studied to determine which group is superior, and on this basis the superior breeding individual is given preference for future breeding purposes. If data are complete, this is an excellent way of identifying superior breeding animals.

(1) Progeny tests are very useful for determining characteristics that are expressed only in one sex, such as milk production in cows or egg production in hens. Even though the bull does not produce milk nor does the rooster lay eggs, they carry genes for these traits and supply one-half of the inheritance of each of their daughters for that particular trait.

(2) Progeny tests are also useful in measuring traits which cannot be measured in the living individual. A good example of this is carcass quality in cattle, sheep, and hogs.

(3) Progeny tests are also being used at the present time by experiment stations in studies of reciprocal recurrent selection. This type of selection

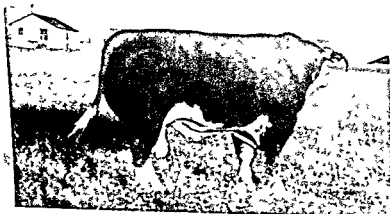


FIGURE 36 THIS BULL Sired 600 CALVES IN ONE YEAR WITHOUT PRODUCING A SINGLE DWARF CALF. WHEN HIS SONS AND DAUGHTERS WERE USED FOR BREEDING, THEY PRODUCED MANY DWARF CALVES. IT TAKES A WELL PLANNED AND ACCURATE PROGENY TEST TO PROVE A SIRE.

TABLE 14

INFLUENCE OF THE BOAR ON THE PERFORMANCE
AND CARCASS QUALITY OF HIS PIGS*

No. of sire	Performance			Carcass			
	No. of offspring	Age at 200 lbs.	Feed/100 gain, birth to wean.	No. of offspring	Backfat thickness	% lean cuts	Loin equiv.
1	8	139	329	4	1.44	55.4	54.2
2	8	150	341	4	1.53	54.2	53.2
3	8	153	334	4	1.56	53.7	52.4
4	8	154	327	4	1.56	54.2	52.9
5	8	153	332	4	1.73	53.3	51.6
6	7	155	337	4	1.64	52.5	50.4
7	8	152	336	4	1.55	51.3	49.4
8	8	148	347	4	1.42	55.9	54.6
9	8	152	343	4	1.53	55.2	56.2
10	16	134	333	8	1.44	55.1	53.7
11	8	143	342	4	1.51	54.5	53.2
12	8	141	329	4	1.55	53.6	51.6
13	8	144	346	4	1.66	54.1	52.0
14	15	150	364	4	1.57	53.4	51.8

Differences between sires as to (1) age at 200 lbs., (2) percentage of lean cuts, and (3) loin equivalent were significant ($P < .01$). The prevailing price for loins times the loin equivalent gives the value of live hogs per 100 pounds body weight.

*Adapted from U. of Mo. Progress Report 22, April 10, 1953.

is used to test for the "nicking ability" of individuals and lines and is based on the performance of the line-cross progeny. Selection of this nature is for traits that are lowly heritable and in which nonadditive gene action seems to be important. It was discussed in detail in Chapter 14.

In comparing individuals on the basis of their progeny, certain precautions should be taken to make the comparisons fair and accurate. In conducting a progeny test, it is very important to test a random sample of the progeny. It would be more desirable if all progeny could be tested, but where this cannot be done, as in litters of swine, those nearer the average of the litter should be tested. It is also important that the females to which a male is mated should be a nonselected group. One would expect the offspring of a sire to be superior if he is mated to the outstanding females in the herd. Such a practice would be misleading in comparing males by a progeny test, since much of the superiority of the offspring of one male could come from the dams and not from the sire. Some breeders prefer using a rotation of different dams when testing males, but this is practical only in swine, where two litters may be produced each year.

Using a large number of offspring in testing a sire increases the accuracy of the test, as a general rule. Where the number of females in a herd

is limited, however, the number of males that may be progeny tested will be less as the number of matings per sire is increased. The point is then, that the breeder must make some decision as to how many sires to test and how many progeny must be produced to give a good test. The number of offspring required for an accurate progeny test will depend upon the heritability of a trait, with fewer offspring being required if the trait is highly heritable, and more being required if it is lowly heritable.

To make accurate progeny tests it is also important to keep the environment as nearly as possible the same for the offspring of the different sires. In progeny testing swine, for instance, confusion would result if the progeny of one sire were fed in dry lot during the summer and the progeny of another were fed on pasture. This would be particularly true in progeny testing for rate of gain where pigs fed modern rations often grow considerably faster in dry lot than on pasture. If this environmental condition were not controlled, the inferior sire might actually be thought to be superior.

Progeny tests in most of our farm animals have certain definite limitations. In cattle, especially, it takes so long to prove an animal on a progeny test that he may be dead before the test is completed and his merit actually known. Progeny tests may be obtained more easily in swine than in other farm animals, but even here the males are usually disposed of by the time they are thoroughly progeny tested.

The process of progeny testing may be speeded up by testing males at an earlier age than they would ordinarily be used for breeding purposes. By hand mating them to a few females or by using them on a larger number of females by artificial insemination, harmful effects that might occur from overuse at too early an age may be prevented.

Too often, farmers send their old sires to market just as soon as their daughters are old enough to breed, in order to prevent inbreeding. This practice has resulted in much loss of good genetic material for livestock improvement. Actually, a sire is not proved until his daughters come into production. Rather than being slaughtered, a sire that has proved himself to be of high genetic merit should be used more extensively. It is true that his usefulness in a particular herd may be finished when his daughters are of breeding age, but he should be sent to another herd to be used for additional breeding purposes.

To be proved, a sire must have completed a satisfactory progeny test record of some kind. For example, he may be considered proved if he has six offspring who have completed one year's record, but this varies with the traits involved. This may be a lactation record, or one of litter size, egg production or birth and weaning weights. A sire so tested may be said to be proved whether his offspring are good or poor. Before buying a proved sire to use in a herd, a breeder should not neglect to find out if he has been proved a good or a poor producer.

Recent research work indicates that, in the future, newer methods of progeny testing may be developed that are superior to those that now exist. For instance, the semen of a bull that has been proved highly superior could be collected at regular intervals, frozen, and stored for later use, even after his death. Some breed associations, however, do not allow this procedure to be followed; instead, they cause the frozen semen to be destroyed when the male dies. In swine, it might be possible to get quicker progeny tests on females by weaning their pigs at two or three weeks of age and breeding them again as soon as possible to produce three litters per year. By the injection of certain hormones a female can be made to produce hundreds of eggs instead of the usual one or few. Research workers have attempted to transplant these extra ova to other females, where the fertilized ova may develop to birth and possess the characteristics of the mother which ovulated the egg. The success of the transplantation of ova has been limited, but future studies may make it more practical. If this could be done, it would be possible for an outstanding female to have many offspring in one year, rather than one or just a few.

METHODS OF SELECTION

In the preceding sections of this chapter, the importance of the merit of the individual and its relatives in identifying genetically superior breeding animals was discussed. Our discussion now will be directed toward the methods of selection that may be practiced, using the information obtained from records on the individual and/or its relatives. It should be kept in mind when selection methods are being discussed that the amount of progress made, regardless of the method used, also depends upon the size of the selection differential (selection intensity), the heritability of the trait, the length of the generation interval, as well as some other factors. These will be discussed in more detail in Chapter 16.

From the practical standpoint, the net value of an animal is dependent upon several traits that may not be of equal economic value or that may be independent of each other. For this reason, it is usually necessary to select for more than one trait at a time. The desired traits will depend upon their economic value, to a great extent, but only those of real importance should be considered. If too many traits are selected for at one time, less progress will be made in the improvement of any particular one. Assuming that the traits are independent and their economic value and heritability are about the same, the progress in selection for any one

trait is only about $\frac{1}{\sqrt{n}}$ times as effective as it would be if selection were applied for that trait alone. For example, if four traits were selected for at one time in an index, the progress for one of these traits would be on the order of $\frac{1}{2}$ (not $\frac{1}{4}$) as effective as if it were selected for alone.

Several methods may be used for determining which animal should be saved and which should be rejected for breeding purposes. Three of these methods which are generally used have been discussed by Hazel and Lush²

TANDEM METHOD

In this method, selection is practiced for only one trait at a time until satisfactory improvement has been made in this trait. Selection efforts for this trait are then relaxed, and efforts are directed toward the improvement of a second then a third, and so on. This is the least efficient of the three methods to be discussed, from the standpoint of the amount of genetic progress made for the time and effort expended by the breeder.

The efficiency of this method depends a great deal upon the genetic association between the traits selected for. If there is a desirable genetic association between the traits, so that improvement in one by selection results in improvement in the other trait not selected for, the method could be quite efficient. If there is little or no genetic association between the traits, which means that they are inherited more or less independently, the efficiency would be less than if the traits were genetically associated in a desirable manner. Since a very long period of time would be involved in the selection practiced, the breeder might change his goals too often or become discouraged and not practice selection that was intensive and prolonged enough to improve any desirable trait effectively. A negative genetic association between two traits, in which selection for an increase in desirability in one trait results in a decrease in the desirability of another, would actually nullify or neutralize the progress made in selection for any one trait. Therefore, the efficiency of such a method would be low.

0.95 inches of backfat at 200 pounds. If the independent culling method of selection were used, Pig B would be rejected, because it was from a litter of only five pigs. However, it was much superior to Pig A in its weight at five months and in backfat thickness, and much of this superiority could have been of a genetic nature. In actual practice, it is possible to cull some genetically very superior individuals when this method is used.

The independent culling method of selection has been widely used in the past, especially in the selection of cattle for show purposes, where each animal must meet a standard of excellence for type and conformation regardless of its status for other economic traits. It is also used when a particular color or color pattern is required. It is still being used to a certain extent in the production of show cattle and in testing stations. It does have an important advantage over the tandem method in that selection is practiced for more than one trait at a time. It sometimes is also advantageous, because an animal may be culled at a young age for its failure to meet minimum standards for one particular trait, when sufficient time to complete the test might reveal superiority in other traits.

THE SELECTION INDEX

This method involves the separate determination of the value for each of the traits selected for, and the addition of these values to give a total score for all of the traits. The animals with the highest total scores are then kept for breeding purposes. The influence of each trait on the final index is determined by how much weight that trait is given in relation to the other traits. The amount of weight given to each trait depends upon its relative economic value, since all traits are not equally important in this respect, and upon the heritability of each trait and the genetic associations among the traits.³

The selection index is more efficient than the independent culling method, for it allows the individuals which are superior in some traits to be saved for breeding purposes even though they may be slightly deficient in one or more of the other traits. If an index is properly constructed, taking all factors into consideration, it is a more efficient method of selection than either of the other two which have been discussed, because it should result in more genetic improvement for the time and effort expended in its use.

Selection indexes seem to be gaining in popularity in livestock breeding. The kind of index used and the weight given to each of the traits is determined to a certain extent by the circumstances under which the animals are produced. Some indexes are used for selection between individuals, others for selection between the progeny of parents from different kinds of matings, such as line-crossing and crossbreeding, and still others for the selection between individuals based on the merit of their

relatives as in the case of dairy bulls where the trait cannot be measured in that particular individual. Examples of these indexes and how they may be used will be given in later chapters dealing with each species of farm animals.

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Questions and Problems

- 1 When should selection be based largely on individuality?
- 2 Why hasn't selection based on type and conformation resulted in an increase in performance in farm animals?
- 3 What evidence do we have that selection for the most vigorous individuals might favor the selection of those which are the most heterozygous?
- 4 In what ways may pedigrees be useful in selection?
- 5 What are some disadvantages of pedigree selection?
- 6 How may pedigrees be improved for selection purposes?
- 7 Define the meaning of *collateral relatives* and discuss how they may be used in selection.
- 8 When are progeny tests most useful in selection?
- 9 Outline how you would conduct progeny tests with 6 boars and 60 sows available for this purpose.
- 10 What are the limitations of progeny tests in animal breeding?
- 11 What are the important factors which determine how much weight should be given to each trait included in a selection index?
- 12 What are the advantages and disadvantages of the tandem method, the independent culling method, and the total score or index method of selection?

16

Some Factors Which Determine ✓ Selection Efficiency

IN THE LAST TWO CHAPTERS, WE DISCUSSED the meaning of selection, the genetic effects of selection, and selection systems to be used to take advantage of the different kinds of gene action. In this chapter, we shall discuss some of the factors that determine whether or not selection for a particular trait, or traits, is effective.

ABILITY OF THE BREEDER TO FIND SUPERIOR BREEDING ANIMALS

The progress that a breeder makes in selection depends upon his ability to select superior breeding stock. This ability depends to a great extent on the ideals and objectives he has in mind at the beginning of his breeding program. If the breeder has no definite goal and changes his objectives each year or two, he cannot expect to make much progress even after many years of livestock breeding. The establishment of a definite objective requires clear thinking into the future, using certain basic facts which are at hand when the original objectives are formed. At the present time, the demand is great for carcass quality as well as for fast and efficient gains. Possibly the demand for these will increase in the future. The breeder therefore must have as his objectives the production of seed stock of this kind and must use all possible means at his disposal to obtain this objective.

The accuracy of the breeder in selecting superior breeding stock will be increased if he will compare all breeding animals under a standard environment. For instance, as discussed earlier, in swine the breeding stock and the young should both be fed in the same manner so that carcass quality of the two are comparable.

Corrections must be made for such factors as age, age of dam, and sex to increase accuracy. In addition, he will be more accurate if he uses scales, rulers, and other measuring devices whenever possible. Some traits in breeding animals such as type and conformation can be measured only with the eye, and such a measurement in this case will have to be used.

Accurate and detailed records are essential for increasing the accuracy of the breeder in choosing superior breeding animals. Records not only tell what the individual has done, but they also tell something about the merit of his various relatives. Records kept in the head are often misleading, because there is a tendency to pick breeding stock from a favorite cow, sow, or ewe which can readily be remembered. Selection of this kind may often be practiced in spite of the fact that offspring chosen in this manner are inferior to others in the herd.

AMOUNT OF SELECTION PRESSURE APPLIED

The amount of selection pressure applied for a particular trait is known as the *selection differential*. The selection differential is the average difference between the herd average and the average of the individuals within that herd that are kept for breeding purposes. The selection differential is illustrated in Figure 37, using backfat thickness in swine as an example. The average backfat thickness in this group of pigs was 37.5 millimeters at 200 pounds of body weight. From this group, boars and sows were selected that averaged 28.5 millimeters of backfat at 200 pounds. The selection differential is the difference between the average of all pigs in that group (37.5) and the average of the individuals kept for breeding purposes (backfat thickness in sows plus backfat thickness in boars divided by two), or 9.0 millimeters.

In general, the larger the selection differential, the more progress one can expect to make in selection. We would expect parents that averaged 23.0 millimeters of backfat selected from the above population to produce offspring with less backfat than parents which averaged 28.5 millimeters.

A number of factors may affect the size of the selection differential. Among these is the number of animals that can be culled in the process of selecting breeding animals, or the number of animals that need to be kept for replacement purposes. Fewer replacement animals will be required in a herd where the number is being kept the same from year to year than in a herd where the size is being increased each year. In the latter case, perhaps all of the females in the herd may be kept for breeding purposes, whereas in the former only the more desirable females would be retained. The selection differential for males is almost always larger than that for females, since fewer males are needed for breeding purposes and they can be more extreme individuals.

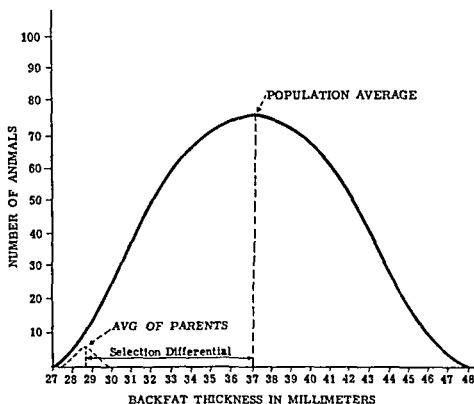


FIGURE 37 ILLUSTRATION OF THE MEANING OF THE SELECTION DIFFERENTIAL USING BACKFAT THICKNESS IN HOGS AS AN EXAMPLE.

The number of traits selected for will have a tendency to reduce the size of the selection differential for any one trait. The reason for this is that an animal which is outstanding in one trait may be mediocre in another or in several others. In other words, it is much more difficult to find an individual that is outstanding for several traits than it is to find one that is outstanding for only one. For this reason, it is important that not too many traits be selected for at one particular time. Only those which are of the greatest economic importance should receive attention, and these should be included in a selection index where each trait selected for is given a certain amount of weight and the overall merit of the animal is expressed as a single numerical value. The weight assigned to each economic trait should be determined on the basis of its relative economic value, its degree of heritability, and whether or not the same genes that affect it affect another trait used in the same index.

A selection index tends to balance the strong points of the animal against its weak points. Progress from selection without the use of an index generally is reduced by the tendency of the herd manager or animal breeder to shift the relative emphasis placed on each of the traits of economic importance from year to year.

Since the increase in the number of traits selected for reduces the size of the selection differential for any one trait, only those of the greatest importance should receive attention, and less importance should be assigned to those such as coat color or size and shape of the ears that have little or no influence on the performance of the individual.

The level of performance of individuals in a herd can affect the size of the selection differential. If selection for a trait has been practiced for many years and the average of the herd for that particular trait is very high, it becomes more difficult to find individuals for breeding purposes that greatly exceed this average. This is especially true for sires that are purchased from another herd. On the other hand, if there has been no selection for improvement in a particular herd and the average for a trait is low, it becomes much easier to find individuals from other herds which exceed this average than it is from a herd where the level of performance is very high. Actually, a sire that may lower the average of the offspring in the first herd may increase the average of the offspring in the second.

To further illustrate how the level of performance may affect the size of the selection differential or the amount of progress made in selection, let us assume that an average of 30 millimeters of backfat in swine is desired. Both boars and sows in a herd are probed for backfat thickness at 200 pounds, but the least amount of backfat in any one individual in this herd is 35 millimeters. Thus, selection within this herd for 30 millimeters of backfat would be extremely slow, because it would not be possible to obtain a large enough selection differential to move rapidly toward the desired backfat thickness. It would be necessary to introduce individuals with thinner backfat from outside the herd if rapid progress in selection toward the desired goal would be realized. Caution should be exercised in selecting individuals from another herd, however, because differences between herds often are largely due to environmental factors. This is less likely to be true of comparisons made within the same herd.

HERITABILITY OF THE TRAITS

The amount of progress that can be made in selection is definitely limited by the heritability of the trait. Selection for a trait that is lowly heritable, such as litter size in swine (15 to 17 per cent heritable), will make little progress. On the other hand, selection for a trait that is highly heritable, such as rate of gain of cattle in the feed lot (about 57 per cent heritable), should result in more progress being made in improving this trait. When the heritability of a trait is high, we expect a larger portion of the selection differential to be due to heredity and less to environment. Where the heritability of a trait is low, most of the selection differential may be due to environmental factors.

Heritability estimates, together with the selection differential, may be used to calculate the progress we can expect to make in selection for a certain trait. For an example, let us use the rate of gain of cattle in the feed lot, which, as mentioned above, is about 57 per cent heritable. Let

us assume that, from a herd that averages 2 00 pounds per day in gain, we select bulls that average 3 00 pounds per day and cows that average 2 50 pounds. We now calculate the selection differential, which is the difference between the average of the parents $(3\ 00 + 2\ 50)/2$, or 2 75 pounds, and the average of all individuals in the herd, which is 2 00 pounds. Thus, the selection differential is 2 75 minus 2 00, or 0 75 pounds. By multiplying the selection differential by the heritability estimate $(0\ 75 \times 57)$, the expected genetic gain in the offspring of the selected parents over the average of the herd from which they came will be 0 428 pounds. In other words, since only about 57 per cent of the advantage of the selected parents is due to genes, only this amount will be transmitted to their offspring. Thus, the offspring would be expected to gain 2 428 pounds per day in the feed lot, if all other things are equal in the two generations.

For further illustration, let us assume that rate of gain in the feed lot had been only 20 per cent heritable instead of 57 per cent. How much progress would we expect to make in selection in one generation, using the same selection differential as used in the first example? In this case, only 20 per cent of the 0 75 pounds, or the selection differential, will be transmitted to the offspring. The expected genetic gain would be $0\ 75 \times 20$, or 0 15 pounds per day in the offspring. The average daily gain of the offspring would be $2\ 00 + 0\ 15$, or 2 15 pounds.

In suggesting the use of heritability estimates in calculating the amount of progress one may expect to make in selection, it is well to point out that heritability estimates are average figures taken from many experiments. Furthermore, in dealing with individuals, it is entirely possible that the superiority of any one parent might be due to a lucky combination of genes or to a more favorable environment. Thus, heritability estimates as used to estimate probable progress one can make in selection for various traits give us a general rather than a specific estimate.

It will be noticed that the average of the offspring in the above example tended to go back, or regress, toward the mean of the population from which the parents were selected. This is known as Galton's law of regression, because he first noted this phenomenon in 1889 in a study of data of 200 parents and 900 of their adult offspring. This law seems to apply to large populations and to a succession of individual cases, as is also true of heritability estimates.

There are at least two reasons for the regression of progeny of extreme parents toward the mean or average of the population. This is particularly true of a trait such as rate of gain which is affected by many genes. The first reason we have already demonstrated when we showed that a portion of the superiority of the parents is due to environment and thus is not transmitted to their offspring. The second reason is that parents may be extreme because of a lucky combination of genes which have a

nicking effect. Such parents are probably highly heterozygous for many genes with a nonadditive effect. Since this heterozygosity of the parents cannot be transmitted as such to their offspring, the desirable combination of genes possessed by the parents is disrupted by segregation and recombination in the offspring, and they regress toward the mean of the population for that particular trait.

GENERATION INTERVAL

The generation interval may be defined as the average age of the parents when their offspring are born. The generation interval will, of course, vary with different species of farm animals and with the procedure followed to produce a new generation of breeding animals. The generation interval in swine can be reduced to one year if pigs are selected from the first litters of gilts bred to boars of the same age. When this is practiced, gilts can be bred when they are seven to eight months of age and will produce litters by the time they are one year of age. If sows as well as boars are progeny-tested before they are used to produce breeding or replacement offspring, the generation interval may be two years or even longer.

In cattle, the generation interval could conceivably be as short as two or three years, but on the average it is considerably longer than this if any progeny-testing is done or if the performance records of cows determine whether or not their offspring are kept for breeding purposes.

To illustrate how the length of the generation interval might affect the amount of progress made in selection, let us compare two systems of breeding in swine, one where young boars and gilts are used for breeding purposes and the generation interval is one year, and one where replacements of breeding stock are selected only after records are obtained on the performance of the parents from two previous litters. The generation interval in the latter case would be about two years. In four years' time, we should have had the opportunity to produce four generations with the first selection system, but with the second only two generations would have been produced. It is obvious that if the heritability of the trait is the same, we would expect to make more progress in selection in four than in two generations.

GENETIC CORRELATIONS AMONG TRAITS

A major gene, or one with large monofactorial effects, can affect two or more traits. For example, in Chapter 11 it was shown that a gene for coat color in some animals often had a detrimental or lethal effect on an individual. This effect of the same gene on more than one trait is known

as pleiotropy. Evidence has also been obtained that two or more quantitative traits, that is, those influenced by many genes with small effects, may also be determined by some of the same genes. When two traits are affected by the same genes, or many of the same genes, they are said to be genetically correlated.

Pleiotropy is probably the major cause of genetic correlations, although it is possible for linkage to have a similar but transitory effect. The existence of genetic correlations among traits has been observed in selection experiments where improvement in one trait was accompanied by a positive or negative genetic change in another for which selection was not practiced. Genetic correlations have also been determined by statistical means, and they give an estimate of the extent to which two traits are affected, or not affected, by the same genes. Whether or not two traits are genetically correlated probably depends upon whether or not they have the same physiological basis.

The genetic correlation between two traits may be very low, which means that probably very few of the same genes affect the two traits. Type and performance in beef cattle is a good example of this in that selection for type seems to have little influence on performance, or vice versa. Obviously, selection on the basis of one will not make an improvement in the other, and we might say that the two traits are inherited independently. If true, this means that it should be possible to get both in our animals, but to do so we must select for both.

Two or more traits may also be correlated from the genetic standpoint in a positive manner. By this is meant that selection for the improvement of one will also result in the improvement in the other even though direct selection for its improvement has not been practiced. An example of this is rate and efficiency of gain in swine. Evidence has accumulated which indicates that if we select within a herd for fast-gaining individuals and make improvement in this trait, the efficiency of gain also improves. This indicates that physiologically, as well as genetically, the two traits are correlated or influenced by the same genes. If the genetic correlation between two traits is high enough, it may not be necessary to measure both, especially if the measurement of one requires added expense, time, and equipment. Thus, if there is a high enough genetic correlation between rate and efficiency of gain, we could measure only rate of gain and select for it and improve both at the same time. The rate of gain of individuals may be measured easily even if animals are fed in a group, but the efficiency of gain is more difficult to measure, since animals must be fed individually and careful attention to prevent feed wastage is required.

It is also possible for two traits to be genetically correlated in a negative manner. This means that selection for the improvement of one, if successful, results in a decline in the other to which it is genetically correlated. An example of such a correlation is butterfat percentage and milk yield in dairy cattle. Although there is evidence of other possible

negative genetic relationships between economic traits in farm animals, more proof is needed. Perhaps negative genetic correlations may explain why selection for dual purpose animals has not been as successful as desired.

CONCLUSIONS ON PROGRESS IN SELECTION

The preceding discussion shows that progress in selection is dependent upon many factors. In short-term selection experiments, the most important of these is the degree of heritability of a trait and the size of the selection differential. Even if the heritability of a trait is as high as 70 per cent, no progress will be made in selection if the selection differential is zero. Furthermore, no progress will be made if the selection differential is large and the heritability of the trait is close to zero. If we expect to make progress in selection, we must be certain that the most effective selection methods are used and that we are selecting for those traits which can be improved.

Questions and Problems

- 1 What can the breeder do to increase his accuracy in finding superior breeding animals?
- 2 What is meant by the selection differential?
- 3 What factors affect the size of the selection differential?
- 4 Why is selection intensity usually greater for males than for females?
- 5 Explain in detail why the offspring of superior parents tend to regress toward the mean of the population.
- 6 The post weaning rate of gain in swine is about 30 per cent heritable. In a herd where the average daily gain is 1.40 pounds, gilts which average 1.70 and boars which average 2.00 pounds of gain are kept for breeding. What would be the expected rate of gain in their offspring?
- 7 Sows in a herd are kept until they produce three litters before replacement gilts are selected. If they are 1 year, 1.5 years, and 2 years of age when they produce their first, second, and third litters, respectively, what would be the generation interval in this herd? (Assume they were mated to a boar of the same age.)
- 8 Calculate the generation interval in your family.
- 9 Explain what is meant by genetic correlations among traits.
- 10 Explain the difference between a positive and a negative genetic correlation.

17

Principles of Inbreeding

INBREEDING IS ANOTHER TOOL, IN ADDITION to selection, that the animal breeder may use for the improvement of farm animals. Inbreeding is a mating system in which progeny are produced by parents more closely related than the average of the population from which they come.

Most livestock producers are familiar with the effects of inbreeding, and they avoid it as much as possible. It is avoided because past experience has shown that inbreeding is usually associated with the appearance of genetic defects and a general over-all decline in vigor and performance. In humans, it is believed that children from the marriage of first cousins are doomed to be deformed physically or mentally, and this belief is so strong that we have certain moral and legal laws which prohibit the marriage of close relatives.

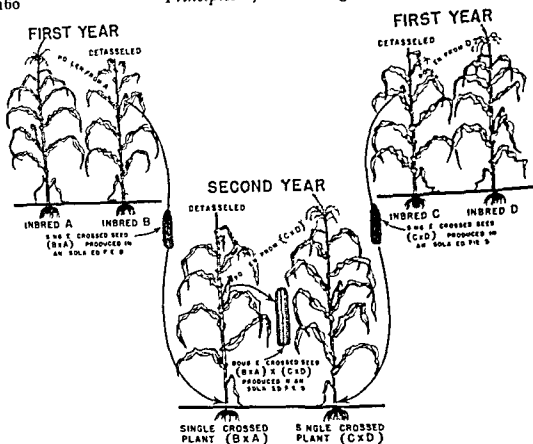


FIGURE 38 DIAGRAM ILLUSTRATING HOW HYBRID SEED CORN IS PRODUCED THE PRINCIPLE INVOLVED IS TO INBREED CORN WHICH NORMALLY IS CROSS-POLLINATED TO FORM SEVERAL INBREED LINES THESE ARE THEN TESTED TO FIND WHICH ONES NICK THE BEST IN CROSSES AND THEN THEY ARE USED AS DIAGRAMMED ABOVE FOR SEED CORN PRODUCTION SOMETHING SIMILAR COULD BE DONE WITH LIVESTOCK (COURTESY OF THE FIELD CROPS DEPARTMENT UNIVERSITY OF MISSOURI)

GENETIC EFFECTS OF INBREEDING

The genetic effect of inbreeding is that it makes more pairs of genes in the population homozygous regardless of the kind of gene action involved. All phenotypic effects of inbreeding result from this one genetic effect so it is very important to understand how homozygosity is brought about.

To illustrate the genetic effect of inbreeding we shall use a single pair of genes and let D be the dominant and d the recessive allele. We shall also assume for this example that we are dealing with plants which are self-fertilized and that there is no selection for or against the dominant or the recessive genes. We will also assume that the parent generation we are working with contains 1600 individuals, all of which are heterozygous for the two genes (Dd). This is shown in Table 15. The crossing of het

TABLE 15
EXAMPLE SHOWING HOW INBREEDING INCREASES THE NUMBER OF PAIRS OF HOMOZYGOUS GENES*

Generation number	Genotype	Per cent homozygous gene pairs	Frequency of d gene	Frequency of dd genotype
0		0	.50	0
1	$\begin{array}{c} 400DD \quad \swarrow \quad \searrow \quad 1600Dd \\ \quad \quad \quad \downarrow \quad \quad \quad \downarrow \\ \quad \quad \quad 800Dd \end{array}$	50	.50	.25
2	$\begin{array}{c} 400DD + 200DD \quad \swarrow \quad \searrow \quad 400Dd \quad \swarrow \quad \searrow \quad 400dd \\ \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \\ \quad \quad \quad 600DD + 100DD \quad \swarrow \quad \searrow \quad 200Dd \quad \swarrow \quad \searrow \quad 200dd \\ \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \\ \quad \quad \quad 700DD + 50DD \quad \swarrow \quad \searrow \quad 100Dd \quad \swarrow \quad \searrow \quad 50dd + 700dd \\ \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \quad \quad \quad \downarrow \\ \quad \quad \quad 750DD + 25DD \quad \swarrow \quad \searrow \quad 50Dd \quad \swarrow \quad \searrow \quad 25dd + 750dd \end{array}$	75	.50	.375
3		87.5	.50	.437
4.		93.8	.50	.468
5		96.9	.50	.484

*Adapted from *General Genetics* by A. M. Srb and R. D. Owen (San Francisco: W. H. Freeman and Company, 1952).

Note: This example assumes self-fertilization with no selection practiced against the recessive gene. Inbreeding in animals where self-fertilization cannot be practiced would progress in the same way, except that homozygosity would be increased more slowly.

erozygous individuals will give a genotypic ratio of 1DD 2Dd 1dd in the first generation. Since the ratio is the important thing to consider, we will keep the number of individuals in each generation at 1600 but will change the ratio as homozygosity increases.

A study of this example will show that in succeeding generations an important change has taken place in the percentage of heterozygotes in the population. In the parent generation, all of the individuals were heterozygous, whereas in the first generation this was true of only 50 per cent of the individuals. Thus we can say that after one generation of self fertilization, the number of individuals in the population that were homozygous was increased by 50 per cent. In this generation, one fourth of all individuals are now homozygous dominant (DD) and one fourth are homozygous recessive (dd).

Now let us continue the inbreeding for more generations by self fertilization. Individuals of the genotype DD when self fertilized will produce nothing but offspring of this same genotype. The same is true of parents of genotype dd. All individuals of genotype Dd, however, will produce offspring again at the genotypic ratio of 1DD 2Dd 1dd. In the second generation of inbreeding we now have the following genotypes 600DD 400Dd 600dd. Seventy five per cent of the individuals are now homozygous dominant and homozygous recessive. Continuing this self fertilization we find that the homozygosity of the population produced increases with each generation but at a decreasing rate.

Other important points are demonstrated in this example. First, note that in the parents the frequencies of both the D and the d genes were 0.50. In the fourth generation the frequency of each gene was still 0.50 showing that inbreeding did not change the frequency of the genes in the population. If we had discarded the individuals of genotype dd or if they had died we would have caused a decrease in the frequency of the d gene. Such an effect would have been due to selection, however, and not to inbreeding as such.

A second point to note in this example is that even though we used only one pair of genes all other pairs of genes that segregate independently are made homozygous at the same rate regardless of their phenotypic effects. Still a third point is that even though the rate of inbreeding is much slower in animals than in plants because self fertilization cannot take place in animals the genetic effects are still the same except homozygosity increases at a slower rate depending upon the degree of relationship between parents which produce inbred offspring.

CONSEQUENCES OF HOMOZYGOSITY

The fact that inbreeding increases the number of pairs of genes that become homozygous regardless of the phenotypic expression of these

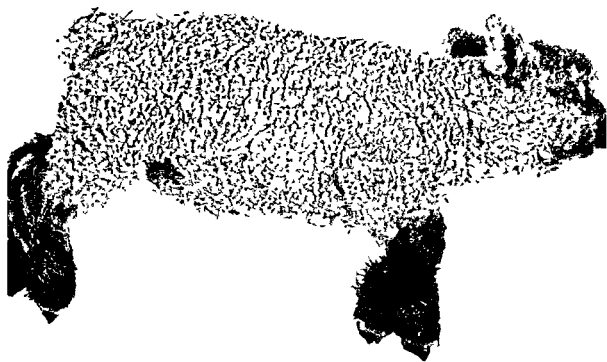


FIGURE 39 DWARF PARROT-MOUTH LAMB A HIDDEN RECESSIVE GENE IN A HERD BROUGHT OUT BY THE MATING OF TWO CARRIERS OF THE RECESSIVE GENE (COURTESY OF THE UNIVERSITY OF MISSOURI.)

genes and how many genes are involved allows us to make certain conclusions regarding this important genetic effect.

Inbreeding does not increase the number of recessive alleles in a population but merely brings them to light through increasing homozygosity. This is well-illustrated in Table 15, where it is shown that even though the frequency of homozygous recessive individuals (dd) increased markedly as inbreeding progressed, the frequency of the d gene did not change from the parental to the fourth generation. In other words, the proportion of recessive genes in the original population was the same as in the fourth generation, but they were hidden by being paired with a dominant gene. Undoubtedly, there are many hidden recessive genes in outbred populations. Dr. H. J. Muller⁶ estimates that the human population now carries an average of eight hidden recessive and semidominant genes per person and the load may be more than this. The same situation probably exists in farm animals. Progeny-test records on six bulls selected at random⁵ showed that each was carrying from one to four detrimental recessive genes.

Inbreeding or increased homozygosity does not uncover dominant genes. This is true because individuals that are heterozygous or homozygous dominant will both show the dominant effect of the gene, and in most cases there is little or no difference in the phenotype of individuals of the two genotypes. Inbreeding, however, does increase the possibility that animals carrying genes with a dominant effect will be homozygous (DD) rather than heterozygous (Dd). Since from the physiological

standpoint dominant genes usually have a favorable effect whereas recessive genes have an unfavorable one, culling the less desirable animals should result in an increase in the frequency of the dominant or favorable genes in the population. This is the reason that the animal breeder who uses inbreeding must be prepared to cull a large proportion of the less desirable individuals from his herd. This requires that a large number of animals be produced in developing a line, and for this reason it is very costly and not too practical in some instances.

Inbreeding fixes characters in an inbred population through increased homozygosity whether or not the effects are favorable or unfavorable. For example, in Table 15 it was pointed out that 47 per cent of the population was homozygous (dd) in the fourth generation of self-fertilization. Inbreeding among such individuals can do nothing but produce dd offspring, and as inbreeding progresses, unless selection against this genotype is practiced, the trait becomes fixed in a larger proportion of the individuals in the inbred line. Many times inbreeding may increase at a rapid rate, and recessive genes may be fixed or made homozygous in many members of the line before much attention is paid to their presence. One inbred line of swine at the Missouri Station¹ had to be discarded because of the presence of a recessive gene for hemophilia that caused many in the line to bleed to death at castration or at farrowing time. The early identification of such defects in an inbred line together with rigid culling and a moderate rate of inbreeding are necessary to prevent the fixation of recessive traits in many of the members of an inbred line. Once they are made homozygous or are fixed in that line, the only cure is to cull known homozygous recessive and heterozygous individuals and their close relatives or to outbreed and introduce the more favorable allele for that trait. The breeder must then backcross to the original inbred line and try to retain the desirable traits of the original line as well as the desirable ones introduced by the outcross.



FIGURE 40 THIS ANIMAL IS AFFLICTED WITH HEMOPHILIA DUE TO AN AUTOSOMAL RECESSIVE GENE IN THE HOMOZYGOUS STATE. INBREEDING UNCOVERED THIS DEFECT IN A LINE OF SWINE. (COURTESY OF THE UNIVERSITY OF MISSOURI.)

Since inbreeding makes more pairs of genes homozygous, the offspring of inbred parents are more likely to receive the same genes from their parents than are offspring of non-inbred parents. This means that the offspring are more likely to resemble the parent from which they receive a dominant gene, and because of this they are more likely to resemble each other. This is another way of saying that inbred parents are more likely to be prepotent than non-inbred parents, at least for traits conditioned by dominant genes. Superior inbred lines should possess more pairs of homozygous dominant genes than inferior inbred lines, since dominant genes are thought to produce more favorable effects.

PHENOTYPIC EFFECTS OF INBREEDING

Inbreeding if accompanied by selection may increase the phenotypic uniformity among animals within an inbred line for traits such as coat color and horns that are conditioned by genes with large monofactorial effects. This is not true, however, of some of the quantitative traits that are affected by many pairs of genes with different modes of expression. Many of these genes seem to act in a physiological manner upon the efficiency of metabolism of many chemical compounds. Studies to date, mostly in swine, point out rather conclusively that increased inbreeding or homozygosity is accompanied by a decline in those traits that are closely related to physical fitness. Among such traits are fertility, viability, and growth rate. Type and conformation may be affected to a certain extent, especially by the occurrence of crooked legs and less bloom shown in inbred animals because they are less vigorous than those which are not inbred.

Inbred animals within an inbred line are more likely to be alike genotypically than phenotypically for traits of economic importance. This is because many inbred animals are not as able to cope with their environment as are those which are not inbred. Many pigs in highly inbred litters are quite variable in size and weight at 154 days of age, whereas pigs from crossbred litters may be more uniform. The variation within inbred litters should be due more to environmental than to genetic causes. When mated to nonrelated animals, inbred animals should breed better than they look, whereas non-inbred animals are often disappointing from the breeding standpoint because they look better than they breed.

PHYSIOLOGICAL BASIS OF INBREEDING EFFECTS

Little is known about the physiological basis of inbreeding effects, because few experiments have been designed to study this in farm ani-

imals Many of the adverse effects of inbreeding in other animals, however, are known to be due to the action of recessive genes, and much is known about the physiology of their action in some instances

As a general rule the action of recessive genes is unfavorable to the well being of the individual This varies from those genes that are lethal in the recessive state to those that have such a slight effect that it can hardly be noticed or may not be noticed at all Undoubtedly, many of the adverse effects of inbreeding are due to several pairs of recessive genes, each of which have only a slight detrimental effect on the same trait Probably the action of most, if not all, such genes is through the failure to produce required enzymes or through the production of abnormal proteins and other compounds

As mentioned previously, inbred animals are usually less able to cope with their environment than are non inbred animals This is shown by greater death losses early in life the lack of the ability to reproduce efficiently in many instances and a slower growth rate and a smaller mature body size Similar effects are often produced by poor nutrition or exposure to many diseases Yet, the above adverse effects are often noted even when efforts are made to supply inbred animals with rations of proper quantity and quality and to control infectious diseases This suggests that the adverse effects of inbreeding may be due to some physiological insufficiency and perhaps to a deficiency or lack of balance of hormones from the endocrine system

Thomas Bates used inbreeding in the development of the Duchess family of Shorthorn cattle Of 58 Duchess cows 24 were barren and the remaining 34 produced only 110 calves during their lifetime The actual reason for their sterility and low fertility was not known, but it must have had a physiological basis and undoubtedly involved genes and the endocrine system

Studies with inbred mice have shown definite differences between inbred lines in certain metabolic and physiological traits For instance, a study of four inbred strains showed a variation in the daily secretion rate of L-thyroxine from 3.5 micrograms per 100 grams of body weight in one line to 6.15 in another²

A study was made with inbred Peppin Merino sheep in which inbred animals were injected with crude pituitary extracts and the effects on growth rate and wool production observed³ This treatment produced a highly significant increase in growth rate in inbred lambs over the first 10 weeks of age when compared with untreated inbred lambs Continued treatment from 10 to 23 weeks of age caused no further change in growth rate Differences between treated and untreated lambs in body weight and size were maintained long after the cessation of treatment The injections caused a significant increase in wool production while they were being given but not afterwards Similar treatments produced no detectable

response in non-inbred lambs. It was concluded that the effect of inbreeding may be attributed at least in part to a reduction in pituitary activity.

Many more studies are needed in which an attempt is made to determine the physiological reason for adverse inbreeding effects. Such studies, although they may be costly, would be helpful in giving us a clearer understanding of the normal physiology of farm animals. Studies are also needed to determine if nutrient requirements of inbred animals are greater than those which are not inbred. Studies such as these might be helpful in increasing the efficiency of production of inbred animals for seed stock purposes.

EFFECT OF INBREEDING ON DIFFERENT KINDS OF GENE ACTION

As far as the genotypes are concerned, increased homozygosity following inbreeding affects all independent pairs of segregating genes in the same way. On the other hand, increased homozygosity following inbreeding may have a quite different effect on the phenotype, depending upon the kind of gene action involved. These effects are illustrated by hypothetical examples in Tables 16 and 17.

DOMINANCE AND RECESSIVENESS

Most geneticists agree that much of the decline in vigor which accompanies inbreeding is due to the uncovering of detrimental recessive genes through increased homozygosity. These recessive genes are hidden by dominant genes in the non-inbred population. If we use a single pair of genes as an example and assign values to the dominant and recessive phenotypes as shown in Table 16, we can see that the average values for the population decrease toward those of the recessive genotypes as the degree of homozygosity increases. We also are assuming here, of course, that there is no selection against the recessive genotypes. Eventually, however, if complete homozygosity were attained, and this is not very likely, there would be no further decrease in the values, because there would be no further uncovering of recessive genes.

In all probability, many pairs of recessive genes may affect the size and vigor of plants and animals, and some may have a greater effect than others. In spite of this, increased homozygosity of many pairs of recessive genes would have a similar effect to that shown in Table 16.

TABLE 16
HYPOTHETICAL EXAMPLE SHOWING THE INFLUENCE OF INBREEDING OR INCREASED HOMOZYGOSITY ON
DIFFERENT TYPES OF GENE ACTION (SELF-FERTILIZATION)*

Number of generation	Genotypes	Population average in units		
		Dominance**	Overdominance***	Additive****
0		180	180	180
1	$ \begin{array}{c} 160Dd \rightarrow \\ \swarrow \quad \searrow \\ 400DD \quad 800Dd \quad 400dd \\ \downarrow \quad \downarrow \quad \downarrow \\ 400DD + 200Dd \quad 400Dd + 400dd \\ \downarrow \quad \downarrow \quad \downarrow \\ 600DD + 100Dd \quad 200Dd + 600dd \\ \downarrow \quad \downarrow \quad \downarrow \\ 700DD + 50Dd \quad 100Dd + 700dd \\ \downarrow \quad \downarrow \quad \downarrow \\ 750DD + 25Dd \quad 50Dd + 750dd \end{array} $	170	160	180
2		165	150	180
3		163	145	180
4		161	143	180
5		161	141	180

*Adapted from *General Genetics* by A. M. Srb and R. D. Owen (San Francisco: W. H. Freeman and Company, 1952).

**Assume that dd gives 140 units and DD and Dd 180 units.

***Assume that dd and DD give 140 units and Dd 180 units.

****Assume that dd gives 160 units, Dd 180 units, and DD 200 units, or that each plus gene D adds 20 units to the residual genotype (dd) of 160 units.

in Table 16. Overdominance, it will be remembered, means that the heterozygous genotypes are superior to either of the homozygotes. Thus, as inbreeding increases, there is a decrease in the number of heterozygous and an increase in the number of homozygous individuals in the population. This will result in a deterioration in a trait affected by this kind of gene action, unless rigid selection is practiced for the more desirable individuals. If we select the superior animals for breeding purposes, however, there would be a tendency to favor those that are the most heterozygous and cull those that are more homozygous. This would result in a slower increase in the degree of homozygosity in the population than one might expect.

EPISTASIS

This type of gene action may also be responsible for the deterioration of a trait when inbreeding is practiced as shown in Table 17. Because epistasis involves the interaction of genes that are not alleles, we must use

TABLE 17

HYPOTHETICAL EXAMPLE SHOWING THE INFLUENCE OF INBREEDING OR INCREASED HOMOZYGOSITY ON EPISTATIC GENE ACTION

Number of generation	Genotypes	Average of population in units
0	1600 <i>AaBb</i>	200
1	{ 100 <i>AABB</i> (200) 200 <i>AABb</i> (200) 100 <i>AAbb</i> (150) 200 <i>AaBB</i> (200) 400 <i>AaBb</i> (200) 200 <i>Aabb</i> (150) 100 <i>aaBB</i> (150) 200 <i>aaBb</i> (150) 100 <i>aabb</i> (150) }	178
2	{ 300 <i>AABB</i> (200) 100 <i>AABb</i> (200) 150 <i>AAbb</i> (150) 100 <i>AaBB</i> (200) 200 <i>AaBb</i> (200) 50 <i>Aabb</i> (150) 200 <i>aaBB</i> (150) 200 <i>aaBb</i> (150) }	172

at least two different pairs of genes to illustrate inbreeding effects on this type of gene action. The mating of individuals of the genotype $AaBb$ could result in offspring of nine possible different genotypes.

The example shown in Table 17 assumes that combinations of the genes A and B are favorable whereas all other combinations are unfavorable. This example shows that there is a decline in the population average following inbreeding if we start with parents which are completely heterozygous for the two genes A and B .

Under actual conditions we have no way of knowing what kinds of epistatic gene action affect the various traits. In this example, if we selected the most desirable individuals for breeding purposes and self-fertilized them, we would move toward fixing the desired combination of genes in the population although the progress made would be very slow. From the theoretical standpoint, developing inbred lines, crossing them, and then developing a new inbred line from the cross should be helpful in fixing a larger number of favorable combinations of genes with epistatic effects. Although this seems possible, it is not too probable and it is doubtful that combinations of many epistatic genes with favorable effects could be fixed in a single inbred line.

ADDITIVE GENE ACTION

In additive gene action, there are no dominant or recessive genes nor are there interactions between the various alleles or pairs of genes. Inbreeding would cause both plus and neutral genes to become more homozygous, but if selection were not practiced as in the example shown in Table 16, there would be no decline in the trait as inbreeding increased. Actually, it seems more likely that if superior individuals were selected when this was the only kind of gene action involved, the merit of the population should improve until genetic variation was exhausted. When this point was reached, no further improvement would result.

If additive gene action were the only kind affecting the important economic traits in farm animals, it would be possible to build superior purebred lines which would breed true for the important traits. Unfortunately, however, different traits of economic importance are affected by both additive and nonadditive gene action, and in many instances both types affect the same trait. Thus, the development of superior inbred lines is by no means simple, and it is necessary to try to fix superior genes in inbred lines and then cross them to get combinations of genes that will give hybrid vigor or heterosis.

POSSIBLE USES OF INBREEDING

The most important factor limiting the usefulness of inbreeding in livestock breeding is the decline in vigor that almost always follows or

accompanies its use. This is doubly important, because the traits affected the most adversely by inbreeding are those of the greatest importance from the economic standpoint. In spite of these disadvantages of inbreeding, there are certain instances where it may be used to advantage in livestock production.

Inbreeding may be used to determine the actual genetic worth of an individual. This is particularly true when a sire that can be mated to 24 to 35 of his own daughters. As mentioned before, such a practice is advantageous because it will test for all recessive genes the sire may be carrying, but at the same time it should give some indication of the desirable genes he may possess. Such a mating system results in 25 per cent inbreeding in one generation and may be too extreme or severe under most conditions. Another disadvantage of this practice is that the male may be dead or no longer in service by the time the test is completed, and he may also fail the test at its completion. This method of testing could be used to advantage in a large herd where artificial insemination could be practiced and where the main objective was *genetic improvement in the stock*.

Inbreeding could be used in a practical way to select against a recessive gene that is of economic importance. Since inbreeding brings out the hidden recessive genes, the homozygous recessive individuals as well as the heterozygotes could be identified and culled. This would require severe culling, however, and might be too costly under most conditions.

Inbreeding may be used to form distinct families within a breed, especially if selection is practiced along with it. Selection between such inbred families for traits of low heritability would be more effective than selection based on individuality alone, especially if there were distinct or definite family differences. Family selection is more effective than individual selection, because it tends to reduce some of the environmental variations that breeders often mistake for those of a genetic nature.

Inbreeding should be used only for the production of seed stock. But even when the breeder uses it for this purpose, he has to determine how much he can sacrifice in the way of lower production and performance to increase the purity of his breeding animals. This becomes more important when we consider the fact that purchasers of breeding stock will pay no more, as a general rule, for inbred stock, because they do not recognize the value of its increased prepotency. On the contrary, the purchaser is more likely to discriminate against inbred sires and dams, because they may be smaller in size for their age, and their conformation may not be as desirable as that of non-inbred animals. In addition, many livestock producers have the mistaken opinion that inbred parents transmit less desirable genes to their offspring than those that are not inbred.

The most practical use of inbreeding at the present time seems to be to develop lines that can be used for crossing purposes, as is done for hybrid seed corn. When two or more inbred lines are found that nick well in crosses, they are more likely than are non-inbred animals to do so in

future crosses because of their purity. The most practical use of inbreeding is to use inbred sires in three-line rotation crosses on crossbred females for commercial production. Inbred females should not be used for commercial production because of their reduced performance as mothers.

From the research standpoint, inbreeding is of value to determine the type, or types, of gene action that affects the various economic traits in farm animals. If inbreeding effects are very great, the trait is affected by nonadditive gene action. If inbreeding effects are very small or nonexistent, the trait is affected mostly by additive gene action. As mentioned in a previous chapter, different methods of selection are required for the two different kinds of gene action.

HOW TO DEVELOP INBRED LINES

Although much more needs to be learned on this subject, there are certain recommendations that can be made on the basis of present information. To develop superior inbred lines, it is imperative that the line be started with outstanding animals that are not carrying detrimental recessive genes. Progeny-tested individuals or those from superior, tested families are the most desirable from this standpoint. The size of the herd used to develop the inbred lines should be large. Possibly several sublines or families should first be developed and those with the greatest merit combined to form one or two inbred lines. In any event, the breeder must be prepared to cull vigorously and must inbreed slowly so those individuals and their relatives that carry detrimental or undesirable genes may be identified and discarded.

References

Questions and Problems

1. Define inbreeding.
2. What is the main genetic effect of inbreeding and how does it affect gene frequencies?
3. Explain what is meant by the statement that inbreeding produces some superior as well as inferior animals.
4. What are the main phenotypic effects of inbreeding?
5. Why doesn't inbreeding uncover dominant genes?
6. Explain why inbred animals within an inbred line may be more alike genotypically than phenotypically for some quantitative traits.
7. What kinds of gene action are responsible for the detrimental effects of inbreeding?
8. What are the possible physiological explanations of the detrimental effects of inbreeding?
9. List some of the possible uses of inbreeding in livestock production.
10. Explain the procedure that should be followed in developing inbred lines of farm animals.
11. Why is it recommended that inbred females not be used for livestock production on a commercial scale?

18

How to Measure Inbreeding and Relationships

BECAUSE INBREEDING HAS SUCH A VERY definite genotypic and phenotypic effect on many important economic traits in farm animals, it is important to know how to measure the amount of inbreeding in a pedigree. This chapter will outline methods of calculating inbreeding and relationship coefficients. The inbreeding coefficient is a measure of the decrease in the proportion of heterozygous genes over what was present before the inbreeding was practiced.

Wright⁷ developed a formula for figuring the inbreeding coefficient by considering the probability that gametes from the sire and dam both carried the same gene. His formula has been modified by Lush,⁴ and this will be discussed as a means of measuring the amount of inbreeding of an individual or a herd. These coefficients may be calculated without preparing arrow diagrams of the pedigree, but the use of these diagrams make calculations easier, so their preparation will be discussed first.

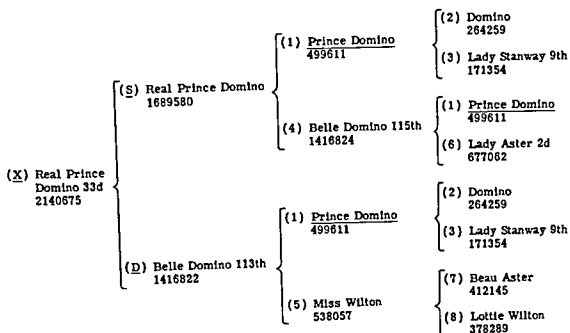
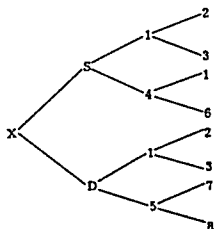


FIGURE 41 PEDIGREE OF REAL PRINCE DOMINO 33RD (2140675), WHICH INCLUDES LETTERS AND NUMBERS TO REPLACE THE NAMES OF THE ANCESTORS TO BE USED IN THE PEDIGREE IN FIGURE 42

numbers replacing the names of individuals in the pedigree, is shown in Figure 42.

The next step is to begin the arrow diagram by placing the letter *X* on a piece of paper along with the sire *S* and the dam *D* in the usual position in the pedigree. Then arrows should be drawn from *S* to *X* and from *D* to *X*, with the arrows pointing to *X* as shown in Figure 43. After this is done, the first common ancestor in the pedigree should be located. A common ancestor is one that appears in both the dam's and the sire's pedigree. Now draw arrows from the common ancestor (1) to the sire, with the arrows pointing toward the sire. Do the same for the dam. If other individuals are between the common ancestor and the sire or dam, they must be included in the arrow pathway in the proper position. The completed arrow diagram of Real Prince Domino 33d as shown in Figure 43 contains

FIGURE 42 PEDIGREE OF REAL PRINCE DOMINO 33RD (2140675), WITH LETTERS AND NUMBERS REPLACING THE NAMES OF HIS ANCESTORS



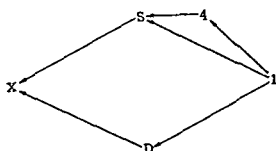


FIGURE 43 ARROW DIAGRAM OF THE PEDIGREE OF REAL PRINCE DOMINO 33RD.

only one common ancestor, which is individual number 1, or Prince Domino. He traces to individual X twice through the sire and once through the dam.

CALCULATING INBREEDING COEFFICIENTS

The formula for calculating inbreeding coefficients is as follows:

$$F_x = \frac{1}{2} \sum \left[\left(\frac{1}{2} \right)^n (1 + F_a) \right],$$

where

F_x refers to the inbreeding coefficient of individual X,
 Σ is the Greek symbol meaning to sum or add all paths,
 n is the power to which one-half must be raised, depending upon the number of arrows connecting the *sire* and *dam* through the common ancestor,
 F_a is the inbreeding coefficient of the common ancestor.

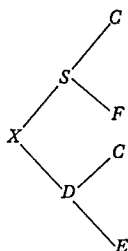
If the common ancestor is not inbred, the formula to use in calculating the inbreeding coefficient becomes:

$$F_x = \frac{1}{2} \sum \left[\left(\frac{1}{2} \right)^n \right]$$

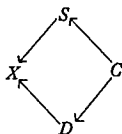
Our first examples will involve calculating inbreeding coefficients for different kinds of matings in which the common ancestor is not inbred; thus the shorter formula will be used.

HALF-SIB MATINGS

The following pedigree and arrow diagram show a half-sib mating, the sire and the dam of individual X having had the same sire (C). The only *common ancestor* in this pedigree is individual C, because he appears in the pedigree of both the sire and the dam of individual X. The arrow



Pedigree



Arrow diagram

diagram shows that there is only one pathway from *C* to *X* through the sire and only one through the dam. This pathway may now be straightened out for illustrative purposes, and it becomes

$$X \longleftarrow S \xleftarrow{1} C \xrightarrow{2} D \longrightarrow X.$$

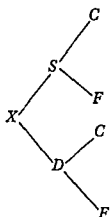
We now number the arrows running from the sire (*S*) through the common ancestor (*C*) to the dam (*D*). We do not count the arrows running from individual *X* to the sire and dam. The number of arrows connecting the sire and dam with the common ancestor is two, and this is the *n* in the formula. Our calculation of the inbreeding coefficient now proceeds by letting

$$F_x = \frac{1}{2}(\frac{1}{2})^2, \text{ or } \frac{1}{2}(0.25), \text{ or } 0.125.$$

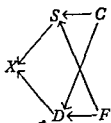
The inbreeding coefficient of individual *X*, then, is 0.125, and this can be expressed as 12.5 per cent by multiplying the inbreeding coefficient by 100.

FULL-SIB MATINGS

The method for calculating the inbreeding coefficient for a full-sib mating is very similar to that described for half-sib matings, except that an additional path and common ancestor are involved. The following pedigree-and-arrow diagram illustrates how calculations are made for such a mating:



Pedigree



Arrow diagram

The two pathways are

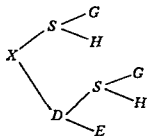
$$X \leftarrow S \xleftarrow{1} C \xrightarrow{2} D \rightarrow X = \left(\frac{1}{2}\right)^2 = 0.25$$

$$\begin{array}{r} X \leftarrow S \xleftarrow{1} F \xrightarrow{2} D \rightarrow X = \left(\frac{1}{2}\right)^2 = 0.25 \\ \hline \text{Totals} \qquad \qquad \qquad 0.50 \end{array}$$

The inbreeding coefficient of individual X is one-half of the sum of these two paths, or $F_x = \frac{1}{2} (0.50) = 0.250$, or 25 per cent inbreeding. Note that in this last pedigree there are two common ancestors (C and F). We merely calculate the figure for all of the pathways, which totals two in this pedigree, from the common ancestors, as denoted by the arrow diagram, and then add or sum all paths, as Σ indicates. Then, when all are added, we take one half of the total to get the inbreeding coefficient.

SIRE \times DAUGHTER MATINGS

The inbreeding coefficient is calculated for parent \times offspring matings in the same manner as for half and full sibs with only slight variations. The following is a pedigree of an individual from a mating of a sire to his own daughter. The inbreeding coefficient from such a mating is 0.25, providing the sire himself is not inbred.



Pedigree



Arrow diagram

The pathway is

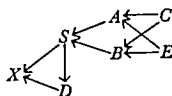
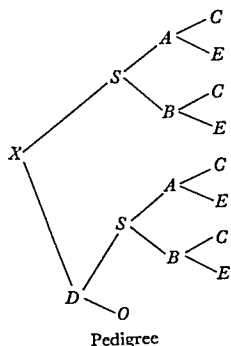
$$X \leftarrow S \xrightarrow{1} D \rightarrow X = \left(\frac{1}{2}\right)^1 = 0.50.$$

Thus, $F_x = \frac{1}{2} (0.50)$, or 0.25, or 25 per cent inbreeding.

Inbreeding coefficients for dam \times son matings are calculated in a similar manner, except the arrow diagrams run from the dam as the common ancestor.

SIRE \times DAUGHTER MATING WITH THE SIRE INBRED

The following pedigree is one in which a sire \times daughter mating is made, but the sire himself is inbred. The first step in calculating the



inbreeding coefficient for such an individual is to complete the arrow diagram as shown.

The first common ancestor in this pedigree, of course, is individual S , which is the sire of individuals X and D . At this point, one might ask what to do about the other common ancestors such as A , B , C , and E ? The answer to this is that we take care of these individuals by first calculating the inbreeding coefficient of individual S or the sire, as was done in the previous example for full-brother \times full sister matings. After this is done, for each path going from individual S to individual D , which is just one in this case, we multiply the path by $(1 + F_s)$, or one plus the inbreeding coefficient of individual S .

The calculation of the inbreeding coefficient for individual S is as follows:

$$\begin{array}{rcl}
 S \leftarrow A \xleftarrow{1} C \xrightarrow{2} B \rightarrow S & = & (\frac{1}{2})^2 = 0.250 \\
 S \leftarrow A \xleftarrow{1} E \xrightarrow{2} B \rightarrow S & = & (\frac{1}{2})^2 = 0.250 \\
 \hline
 \text{Total} & & 0.500
 \end{array}$$

The inbreeding coefficient of individual S , or F_s , would be $\frac{1}{2}$ (0.500), or 0.250, or 25 per cent. We now proceed to calculate the inbreeding coefficient (F_x) of individual X . Only one pathway is involved, and this is

$$X \leftarrow S \xrightarrow{1} D \rightarrow X = (\frac{1}{2})^1, \text{ or } 0.50.$$

Since individual S , which is the common ancestor, is inbred, we must use the complete formula as given earlier. The computations then are $F_x = \frac{1}{2} [0.50 (1.25)] = \frac{1}{2} (0.625)$, or 0.3125. Thus, individual X is 31.25 per cent inbred.

COEFFICIENTS OF RELATIONSHIP

The coefficient of relationship between two individuals is an expression of the probability that they possess duplicate genes, because of their common line of descent, over and above those found in the base population. It is evident that an increase in inbreeding causes the relationship of individuals within an inbred line to increase. On the other hand, it is possible for two different inbred lines to be inbred the same amount but still not be related. For example, individuals in a Landrace line of hogs might be inbred 25 per cent and in a Poland line a similar amount. They do not have duplicate genes in common because of their common descent, although they do possess some of the same genes because they belong to the same species.

It is often of practical importance to know something about the degree of relationship between two individuals. For instance, an animal may be offered for sale that has a pedigree similar to that of another animal that sold earlier at another sale for a high price, and the breeder wants to know the maximum that he should bid for this animal. Or, he may have a bull for sale at private treaty and would like to use the situation described as a sales point. Another instance when relationship coefficients might be of value is when a livestock breeder may have the chance to buy two animals, one of which shows excellent type and comes at a high asking price and the other of which is lacking in some one point but not to the extent to warrant disregarding the animal entirely. If they have a high coefficient of relationship, one would probably perform just as well in the breeder's herd as the other. He could purchase the cheaper animal and produce as good stock with it as with the one which was more expensive.

From the theoretical standpoint, relationships could have another use for the livestock breeder. For traits such as carcass quality that cannot be measured very well until after the death of the individual, the slaughter of a relative should give some indication of the carcass quality of the individual in question. The value of the relative in this respect would be proportional to the degree the two individuals were related. A full brother or sister would be worth more than a half sister or brother in this respect. Full brothers and sisters within an inbred line would also be more closely related than would be full brothers and sisters which are not inbred. Relationship coefficients would give a good indication of the value of records of relatives from this standpoint.

Relationships are of two different kinds. One is collateral relatives, that is, those not related as ancestors or descendants; the other is direct relation, that is, ancestors or descendants. The two kinds will be discussed separately.

RELATIONSHIP COEFFICIENTS BETWEEN COLLATERAL RELATIVES

Methods of calculating relationships are very similar to those used for calculating inbreeding coefficients, and arrow diagrams are of value in this respect. The formula is as follows:

$$R_{xy} = \frac{\sum \left[\left(\frac{1}{2} \right)^n (1 + F_a) \right]}{\sqrt{(1 + F_x)(1 + F_y)}} \quad \checkmark$$

where

R_{xy} is the relationship coefficient between animals X and Y ,

Σ is the Greek symbol meaning to sum or add,

n is the number of arrows connecting individual X with Y through the common ancestor for each path,

F_x is the inbreeding coefficient of animal X ,

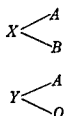
F_y is the inbreeding coefficient of animal Y ,

F_a is the inbreeding coefficient of the common ancestor.

If individuals X and Y and their common ancestor are not inbred, the formula becomes:

$$R_{xy} = \Sigma \left[\left(\frac{1}{2} \right)^n \right].$$

The following is an example in which the relationship coefficient between half brothers and half sisters is calculated. In this example, we shall let individual X be the male and individual Y the female, although relationship coefficients may be calculated for animals of the same sex. Since none of the individuals involved are inbred, we can use the simple form of the formula for calculating the relationship coefficient.



Pedigree



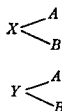
Arrow diagram

$$X \xleftarrow{1} A \xrightarrow{2} Y$$

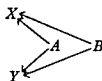
Pathway

The relationship coefficient between individuals X and Y , or R_{xy} , is $(\frac{1}{2})^2$, or 0.250. This means that these two individuals are related by about 25 per cent, or they probably have an increase in this percentage of duplicate genes over that found in the base or non inbred population.

The calculation of the relationship coefficient between full brothers and sisters is similar to the above example, except that there are two common ancestors in such a case, and there are two pathways of gene flow. The calculation of the coefficient of relationship is as follows:



Pedigree



Arrow diagram

$$\begin{array}{l} X \xleftarrow{1} A \xrightarrow{2} Y = (\frac{1}{2})^2 = 0.250 \\ X \xleftarrow{1} B \xrightarrow{2} Y = (\frac{1}{2})^2 = 0.250 \\ \hline \text{Totals} \qquad \qquad \qquad 0.500 \end{array}$$

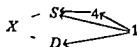
Pathways

 R_{xy}

The relationship coefficient for individuals X and Y in this example is 0.50.

RELATIONSHIP COEFFICIENT FOR THE SIRE AND DAM OF REAL PRINCE DOMINO 33RD

The following is the arrow diagram made from the pedigree of this Hereford bull, as shown in Figure 43:



Real Prince Domino (5) his sire, is inbred, so we must first calculate his inbreeding coefficient which would be 0.250, since he was from a mating of Prince Domino (1) to one of his own daughters (4) Belle Domino 115th. The next step is to list the number of paths through the common ancestor (1) connecting the sire S and the dam D . These would be,

$$\begin{array}{rcl}
 S \xleftarrow{1} 4 \xleftarrow{2} 1 \xrightarrow{3} D & = & (\frac{1}{2})^3 = 0.1250 \\
 S \xleftarrow{1} 1 \xrightarrow{2} D & = & (\frac{1}{2})^2 = 0.2500 \\
 \hline
 \text{Totals} & & 0.3750
 \end{array}$$

The remaining calculations would be

$$R_{sd} = \frac{0.3750}{\sqrt{1 + 0.25 \times 1 + 0}} = \frac{0.3750}{\sqrt{1.25}} = \frac{0.3750}{1.1180} = 0.3354,$$

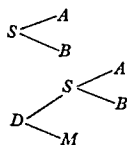
or the relationship between *S* and *D* would be 33.5 per cent.

DIRECT RELATIONSHIPS

Many times it is of interest to know something about the relationship between an individual and some outstanding ancestor in the pedigree. This is of particular value when linebreeding has been practiced, although the same procedure may be used for calculating the degree of relationship to any particular ancestor. The formula used is:

$$R_{xa} = \Sigma (\frac{1}{2})^n \sqrt{\frac{1 + F_a}{1 + F_x}}$$

In this formula, of course, when neither of the individuals involved is inbred, the figures under the square root sign will be equal to one and can be disregarded. For example, the following method is used to calculate the relationship between a sire (*S*) and his daughter (*D*).



Pedigrees

$$S \longrightarrow D = S \xrightarrow{1} D = (\frac{1}{2})^1 = 0.500$$

Arrow
diagram

Pathway

Relationship
coefficient

For further illustration, let us calculate the relationship coefficient between Real Prince Domino 33d (X) and Prince Domino (I). We can use the arrow diagram shown previously. The first step is to calculate the inbreeding of Prince Domino (I), but in this pedigree he shows no in-

breeding Next, we calculate the inbreeding coefficient of Real Prince Domino 33d which is,

$$\begin{array}{rcl}
 X \xleftarrow{1} S \xleftarrow{4} I \xrightarrow{3} D \longrightarrow X & = & (\frac{1}{2})^3 = 0.1250 \\
 X \xleftarrow{1} S \xleftarrow{1} I \xrightarrow{2} D \longrightarrow X & = & (\frac{1}{2})^2 = 0.2500 \\
 \hline
 \text{Totals} & & 0.3750
 \end{array}$$

The inbreeding coefficient is $\frac{1}{2} \times 0.3750$, or 0.1875

The third step is to list all paths connecting Real Prince Domino 33d (C) with Prince Domino (1), which are,

$$\begin{array}{rcl}
 X \xrightarrow{1} S \xrightarrow{2} 4 \xrightarrow{3} 1 & = & (\frac{1}{2})^3 = 0.1250 \\
 X \xrightarrow{1} S \xrightarrow{2} 1 & = & (\frac{1}{2})^2 = 0.2500 \\
 X \xrightarrow{1} D \xrightarrow{2} 1 & = & (\frac{1}{2})^2 = 0.2500 \\
 \hline
 \text{Totals} & & 0.6250
 \end{array}$$

The figure 0.6250 expresses the probable proportion of genes individual X inherited from ancestor 1. The final relationship coefficient is calculated from

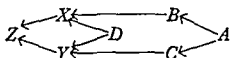
$$\begin{aligned}
 R_{X1} &= 0.6250 \sqrt{\frac{1+0}{1+0.1875}} = 0.6250 \sqrt{\frac{1}{1.1875}} = 0.6250 \times \sqrt{0.8421} \\
 &= 0.6250 \times 0.9177 = 0.5736
 \end{aligned}$$

This coefficient represents the probability that individuals X and 1 will have duplicate genes which were unlike in the base or non inbred population

COVARIANCE TABLES FOR MEASURING INBREEDING COEFFICIENTS

In some herds such as experimental herds where inbreeding is being practiced, covariance charts for all animals within the inbred line may be calculated in the early stages of the development of the inbred line. Once these are established, it is fairly simple and rapid to calculate inbreeding coefficients for different individuals.²

To illustrate the calculation of covariance charts, let us use the following pedigree for individual Z which is given in the form of an arrow diagram. The first step is to list all animals in the order of their birth and also the parents of each individual, as is done in Table 18.



Note that this pedigree does not list the parents of individuals *A* or *D*, because they are not inbred. One parent (individual *A*) is shown for both *B* and *C*. Both parents are shown for individuals *X* and *Y*, because they are involved in the inbreeding of individual *Z*. The component for any covariance cell in Table 18 between any two individuals is one-half of the components of the parents of that individual. For instance, the covariance for *A* and *B* is $\frac{(1 + 0)}{2} = 0.50$. Other components are calculated

as follows:

For *A* and *D* it is 0, because the parents are not related.

For *B* and *Y*, it is $\text{cov} \frac{R_{BD} + \text{cov } R_{BC}}{2}$ or $\frac{0 + 0.25}{2} = 0.125$.

For *B* and *Z*, it is $\text{cov} \frac{R_{BX} + \text{cov } R_{BY}}{2}$ or $\frac{0.50 + 0.125}{2} = 0.3125$.

For *X* and *Y*, it is $\text{cov} \frac{R_{XD} + \text{cov } R_{YC}}{2}$ or $\frac{0.50 + 0.125}{2} = 0.3125$.

For *X* and *Z*, it is $\text{cov} \frac{R_{XX} + \text{cov } R_{XY}}{2}$ or $\frac{1.00 + 0.3125}{2} = 0.6563$.

TABLE 18

COVARIANCE CHART CONSTRUCTED FOR INDIVIDUALS IN THE PEDIGREE OF INDIVIDUAL *Z*

Sire		A	A		D	D	X
Dam					B	C	Y
Individuals	A	B	C	D	X	Y	Z
A	1.000	0.500	0.500	0	0.250	0.250	0.250
B		1.000	0.250	0	0.500	0.125	0.313
C			1.000	0	0.125	0.500	0.313
D				1.000	0.500	0.500	0.500
X					1.000	0.313	0.656
Y						1.000	0.656
Z							1.156

Note: The inbreeding coefficient for individual *Z*, for example, is one-half the coefficient of relationship of the parents (0.313), or 0.1563.

TABLE 19

COVARIANCE CHART FOR INDIVIDUALS IN AN
INBRED LINE OF DUROC SWINE

Sire	24	10	10	10	241	251	303	303	303	303	303
Dam	75	36	36	36	346	540	43	47	49	136	144
Individuals	303♂	43♀	47♀	49♀	136♀	144♀	1♂	2♀	3♀	4♀	5♀
303♂	1 000	0	0	0	0	0	0 500	0 500	0 500	0 500	0 500
43♀		1 000	0 500	0 500	0	0	0 500	0 250	0 250	0	0
47♀			1 000	0 500	0	0	0 250	0 500	0 250	0	0
49♀				1 000	0	0	0 250	0 250	0 500	0	0
136♀					1 000	0	0	0	0	0 500	0
144♀						1 000	0	0	0	0	0 500
1♂							1 000	0 375	0 375	0 250	0 250
2♀								1 000	0 375	0 250	0 250
3♀									1 000	0 250	0 250
4♀										1 000	0 250
5♀											1 000

Note The inbreeding of the offspring out of any one male and female in this chart would be one half of the covariance component. For example offspring from a mating between male 1 and female 2 would be one half of 0 375 or 0 1875

All diagonal cells in the covariance chart are calculated from $1 + F_z$, where F_z is equal to one half of the covariance between the parents of an individual. Thus the inbreeding coefficient of individual Z would be one half of the covariance between individuals X and Y, or one-half of 0 3125, or 0 15625. The diagonal component for individual Z then becomes $1 + 0 15625$.

If no inbreeding is involved the coefficient of relationship may be read directly from the charts or the off-diagonal cells. If inbreeding is involved corrections must be made for inbreeding by using the formula,

$$R_{yz} = \frac{\Sigma (\frac{1}{2})^n (1 + F_z)}{\sqrt{1 + F_x} \sqrt{1 + F_y}}$$

For example the relationship coefficient for Y and Z would have to be corrected for the inbreeding of Z as follows

$$R_{yz} = \frac{0 6563}{\sqrt{1 + 0} \sqrt{1 + 0 1563}} = \frac{0 6563}{1 075} = 0 610$$

For further illustration, let us use data from an inbred line of Duroc swine maintained at the Missouri Agricultural Experiment Station. Boar 303 and sows 43, 47, 49, 136, and 144 will be used in this example. None of the original stock was inbred or related, except sows 43, 47, and 49, which were littermates. The covariance chart for offspring of the five sows bred to boar 303 is given in Table 19. The inbreeding of any offspring from male 1 mated to either females 2, 3, 4, or 5 could be calculated by taking one-half of the covariance component from the off-diagonal cells. The relation coefficients and inbreeding coefficients among descendants of the original stock would be easily calculated by extending the covariance chart. In doing this, however, the covariance components for any two individuals should be corrected for inbreeding as described previously.

OTHER METHODS OF ESTIMATING HOMOZYGOSITY IN A POPULATION

Blood types in animals have received some attention from research workers as a possible means of estimating the degree of homozygosity within certain inbred lines. The *B* blood group system is of considerable interest in this respect, because a very large number of alleles is known to be present at this locus on the chromosomes.⁵ If a high degree of inbreeding is involved, there should be a reduction in the number of alleles in this group found in an inbred line.

Blood antigen studies were made at the Colorado Experiment Station in the formative years of the development of inbred lines of beef cattle.⁶ It was found that the incidence of certain antigens was high in some lines but almost totally absent in others. The rate of disappearance of the antigens from the inbred lines was faster than the predicted rate, based on the loss of heterozygosity estimated by means of Wright's inbreeding formula.

In a study with poultry,² it was found that the number of alleles at the *B* locus was reduced to two when inbreeding was 66 per cent or more. On the other hand, up to eight alleles were present in non-inbred populations.

It is possible that inherited characteristics other than blood types may be used to estimate the degree of homozygosity of individuals within a line or strain, but little research has been done along this line. It has been suggested that nipple numbers in swine might give a rough estimate of the homozygosity within an inbred line, although this trait is apparently affected by several pairs of genes some of which have an additive and some a nonadditive action.¹ It seems very unlikely that environment would have much influence on nipple numbers in swine, and so the variations observed must be largely due to heredity. That individuals

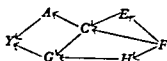
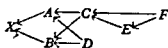
within some inbred lines do vary less in nipple numbers than those in other lines was shown by a coefficient of variation of 5.70 per cent in an inbred Landrace line as compared to 8.22 per cent in another line of inbred Polands. No study was made of changes in variation in nipple numbers as inbreeding increased.

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Questions and Problems

1. Explain what is meant by an inbreeding coefficient.
2. Explain what is meant by a relationship coefficient.
3. Of what use are inbreeding and relationship coefficients?
4. Compute the inbreeding coefficients for individuals X and Y in the following pedigrees.



5. Compute the relationship coefficients for individuals X and Y in the above pedigrees.
6. What is the relationship between individuals Y and F in the second pedigree?

19

Linebreeding

LINEBREEDING IS A SYSTEM OF MATING in which the relationship of an individual, or individuals, is kept as close as possible to some ancestor in the pedigree. The ancestor is usually a male rather than a female, because a male generally produces many more descendants than a female, and this allows a greater opportunity to prove his merit by means of a progeny test.

ILLUSTRATION OF LINEBREEDING

Pedigree 1 in Figure 44 illustrates systematic linebreeding. This is a hypothetical pedigree, with letters and numbers used in place of names to simplify the example. Only one ancestor in this pedigree is responsible for the relationship between the sire and the dam of individual X. This is ancestor 5. We have purposely placed him in this pedigree as the only great grandfather of individual X. The arrow diagram shows that individual X traces by four separate lines to his ancestor 5. This is why it is called linebreeding. If linebreeding or inbreeding had not been practiced, there would have been only one line involved. In this pedigree, individual X probably received about 50 per cent of his inheritance from ancestor 5. This is approximately as much as an individual usually receives from a parent. If linebreeding had not been practiced, individual X would have received only about 12.5 per cent of his inheritance from individual 5.

An actual pedigree of Real Prince Domino 13th, a Hereford bull, together with an arrow diagram of this pedigree is given in Figures 45 and 46. Since Real Prince Domino 13th traces by several paths to Prince Domino, we would say that he is linebred to Prince Domino. He also traces by two paths to Beta Aster, but apparently no great attempt has been made to keep the relationship high to this ancestor, whereas it is obvious that a deliberate attempt has been made to do so as far as Prince Domino is concerned.

PEDIGREES AND ARROW DIAGRAMS OF THE PEDIGREES WHICH ILLUSTRATE SOME DIFFERENT SYSTEMS OF LINEBREEDING

No of pedigree	Pedigree	Arrow diagram	Inbreeding coefficient	% inher from S*	Relationship coefficient**
1/			125	50	47
2/			.0625 094	37.5	36
3			031	25.0	25
4			219	50.0	45
5			✓ 375	87.5	78 ✓

Several different procedures for linebreeding may be followed, but they must be planned in advance. Some of these systems are illustrated in Figure 44. In pedigree 1, half-sib matings have been made in the pedigrees of the sire (S) and the dam (D), with four individuals being used in that mating that are half sibs. In pedigree 2, half-sib matings were used to produce the sire but not the dam, but the sire of the dam (D) is a half brother of the parents of the sire of individual X. In pedigree 3, the sire and dam of X are related only because their sires were half brothers. In these examples, the relationship between X and 5 becomes less and less as the number of paths connecting them decreases. Individual X is not highly inbred in any of these three pedigrees. Even in pedigree 1, where it seems to be high, it is only 0.125.

Pedigree 4 in Figure 44 illustrates linebreeding to ancestor 5 through a single son, individual 1. The relationship of X and its ancestor 5 in this pedigree is about the same as it was in pedigree 1. For this reason, there would be an advantage of only one son of ancestor 5 being required in this pedigree, whereas in pedigree 1, two sons were required. The disadvantage of the system illustrated in pedigree 4 is that the inbreeding coefficient of individual X would be about 0.22, or considerably higher

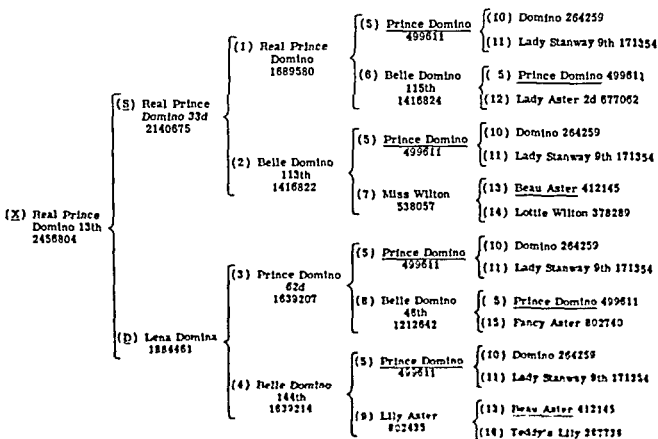


FIGURE 45 PEDIGREE OF REAL PRINCE DOMINO 13TH, SHOWING LINEBREEDING TO PRINCE DOMINO.

Linebreeding

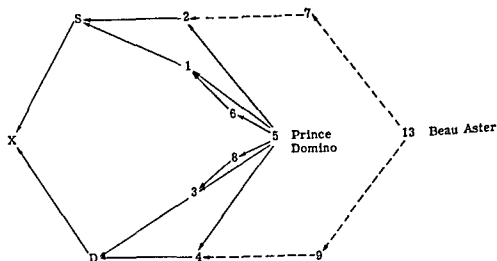
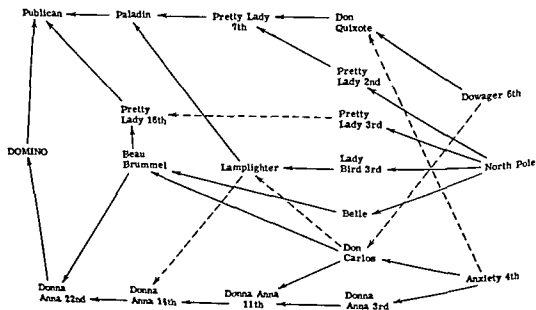


FIGURE 46 ARROW DIAGRAM OF THE PEDIGREE OF REAL PRINCE DOMINO 13TH SHOWING INTENSE LINEBREEDING TO PRINCE DOMINO AND VERY MILD LINEBREEDING TO BEAU ASTER.

than in pedigree 1. Since the inbreeding coefficient would be higher, the offspring might be less vigorous and more recessive genetic defects might appear in the offspring in this pedigree than in pedigree 1.

Pedigree 5 in Figure 44 is a system of linebreeding in which a sire is mated to two successive generations of his own daughters. Such a system would certainly result in a high relationship between individual X and ancestor S, but the inbreeding coefficient would be high, which might be

FIGURE 47 ARROW DIAGRAM OF THE PEDIGREE OF DOMINO SHOWING THE SYSTEM OF LINEBREEDING AS USED BY GUDGELL AND SIMPSON



undesirable. This system illustrates a situation in which linebreeding could be practiced while the ancestor to which linebreeding was directed was still alive, whereas the other systems would more likely be used after the ancestor was dead.

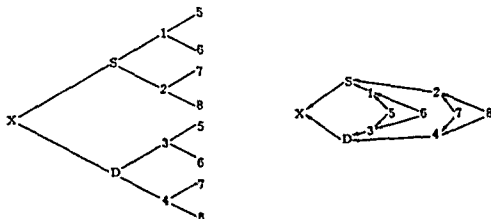
Linebreeding to a single ancestor cannot be carried on for many generations without recurrent linebreeding through a descendant, as illustrated in pedigree 4. The arrow diagram of the extended pedigree of Domino given in Figure 47 shows the system used by Gudgell and Simpson, early American breeders of Hereford cattle, in which there was linebreeding to several different ancestors, with a blending of the inheritance of these to produce this particular individual.

COMPARISON BETWEEN ORDINARY INBREEDING AND LINEBREEDING

Inbreeding is a system of mating in which offspring are produced by parents that are *more closely related than the mean of the population* from which they come. This definition also applies to linebreeding, because linebreeding is a special form of inbreeding. However, in linebreeding, as defined earlier in this chapter, the relationship of an individual is kept close to a particular ancestor.

Inbreeding other than linebreeding is a system of mating in which related parents are mated with no particular attempt to increase the relationship of the offspring to any one particular ancestor in the pedigree. This concept is illustrated in Figure 48. A comparison of this pedi-

FIGURE 48 THIS HYPOTHETICAL PEDIGREE AND ITS ARROW DIAGRAM ILLUSTRATE A FORM OF INBREEDING THAT IS NOT LINEBREEDING BECAUSE FOUR DIFFERENT COMMON ANCESTORS (5, 6, 7, AND 8) ARE RESPONSIBLE FOR THE RELATIONSHIP BETWEEN THE SIRE (S) AND THE DAM (D). INDIVIDUAL (X) HAS AN INBREEDING COEFFICIENT OF .125, AND THE PROBABLE AMOUNT OF INHERITANCE RECEIVED BY X FROM ANY ONE OF THE COMMON ANCESTORS IS 12.5 PER CENT.



gree with pedigree 1 in Figure 44 illustrates the basic difference between linebreeding and ordinary inbreeding. The arrow diagram of the pedigree in Figure 48 shows that four different ancestors are responsible for the inbreeding of individual X. The inbreeding coefficient of X in Figure 48 is also 0.125 as in pedigree 1 in Figure 44, but the inheritance received by individual X from any one ancestor is only about 12.5 per cent. Thus, in the mating system illustrated in Figure 48, no attempt was made to concentrate the inheritance of any one ancestor.

The genetic effects of linebreeding are the same as those of inbreeding explained in Chapter 17. Thus, linebreeding tends to make pairs of genes carried in the heterozygous condition in the ancestor more homozygous in the linebred offspring. In addition, linebreeding increases the probability that the linebred offspring will possess the same genes as the ancestor to which linebreeding is directed. If the ancestor possessed many desirable genes, the offspring are more likely to possess these same desirable genes. If he possessed detrimental recessive genes in the heterozygous state, the offspring are more likely to possess them. Linebreeding will bring some of these recessive genes together in the homozygous state in some of the offspring. This serves to emphasize the importance of linebreeding to an ancestor that is superior genetically and carries a minimum of detrimental recessive genes. Accurate and adequate progeny tests help to identify such individuals.

When ordinary inbreeding is practiced, the relationship between the sire and dam often depends upon several common ancestors. It is evident that it is more difficult to distinguish three or four genetically superior ancestors than it is to distinguish one. A larger number of ancestors increases the probability of a wider variety of homozygous detrimental recessive genes appearing in the offspring when inbreeding is practiced.

WHY BREEDERS FAVOR LINEBREEDING OVER INBREEDING

Linebreeding is often looked upon with favor by breeders, but inbreeding is not, probably because linebreeding is usually not so intense, and when it is used, the inheritance of truly outstanding individuals is concentrated in the pedigree. Perhaps, also, the name of some great show animal in the pedigree has caused breeders to remember the superior individuals produced by linebreeding and to overlook others which were less superior.

Although when linebreeding is practiced, inbreeding is usually not intense, it can be if a linebreeding system such as that illustrated in pedigree 5 in Figure 44 is used, where a male is mated to his own daughters. The first generation of such a mating would result in an inbreeding coefficient of 0.25, which is intense enough to cause a decline

in the vigor of the offspring produced and an appearance of genetic defects. Two instances in which Prince Domino was mated to his own daughters is shown in the pedigree of Real Prince Domino 13th in Figure 45.

As a general rule, a sire is not mated to his own daughters when linebreeding is practiced but half sib matings are made among the offspring of this particular sire. Perhaps this is done because the breeder wants to avoid intense inbreeding or because he has not yet recognized the outstanding merit of the ancestor in question. On the other hand there may be no great need for linebreeding at that stage, since the offspring of a parent are related to that parent by about 50 per cent.

Linebreeding is often used after the death of the ancestor or when it is no longer available for breeding purposes. Then the half sib matings would be the closest possible matings in a linebreeding program. Full sib matings would be possible in litter bearing animals such as swine but this would be no more effective at least at the beginning of the linebreeding program, than half sib matings in increasing the relationship to one particular ancestor in the pedigree. The disadvantage of full sib matings would be that the inbreeding coefficient of the first generation would be 0.25, as compared to 0.125 in the half sib matings and there would be a possibility of the offspring getting detrimental recessive genes from at least two common ancestors instead of from one ancestor.

LINEBREEDING IN THE PAST

Linebreeding was used extensively in the development of the British breeds of cattle, such as the Angus, Herefords and Shorthorns. This system was also used by the King Ranch in Texas in the development of the Santa Gertrudis breed of cattle. Mr. Gentry of Sedalia, Missouri, who was a successful breeder of Berkshire hogs in the early 1900's made use of this system of breeding in producing many show ring winners.

Linebreeding and inbreeding were used to a great extent by early breeders of Hereford cattle in England. Benjamin Tomkins and his son in the 1700's used such a system of mating to improve their cattle as did William and John Hewer to obtain the desired color and type. Lord Berwick, another notable early breeder of Herefords in England, improved his herd by purchasing and using the bull, Sir David (319). He was probably the greatest show bull of his day and was from an accidental mating of a cow to her own sire.

Early breeders of Herefords in the United States also used linebreeding and inbreeding to improve their cattle. One of the most famous of the herds which followed this course was that founded by Gudgell and Simpson, at Independence, Missouri. They imported foundation cattle from

England, and among the imports were the bulls, Anxiety 4th and North Pole. They tried outbreeding at first but apparently were disappointed in the results, for they later turned to linebreeding. They concentrated and blended the inheritance of Anxiety 4th and North Pole to develop one of the most outstanding herds in the United States. The pedigree of Domino in Figure 47 shows the system of breeding used by Gudgell and Simpson. Actually, this pedigree shows that Domino was linebred to three different ancestors, Anxiety 4th, North Pole, and Dowager 6th, receiving a probable 20 to 24 per cent of his inheritance from each of them. Even though it would appear that Domino was very highly inbred, the inbreeding coefficient calculated from this pedigree is only about 0.17.

WHEN TO LINEBREED

Linebreeding should be used only in a purebred population of a high degree of excellence. Its use is indicated when some truly outstanding individual has been identified and proved by an adequate progeny test. If such an individual is still living and available for breeding purposes, it seems more desirable to use him on females which are not related to him, since all of his offspring from such a mating will receive about 50 per cent of their inheritance from him anyway. If he is mated to his own daughters, the relationship coefficient between him and the offspring will be about 0.67. The inbreeding coefficient for the offspring will be 0.25 and high enough to increase the probability of a decline in vigor and the appearance of genetic defects.

Linebreeding is probably most useful when the outstanding individual is dead or not available for breeding purposes. One of the systems of linebreeding illustrated in Figure 44 could be used with the main objective of concentrating the genes of that ancestor in the herd or flock. This requires a planned, systematic mating system. If practiced for a long period of time, linebreeding sooner or later must be directed through one or more of the ancestor's sons or other descendants, as illustrated in pedigree 4 in Figure 44.

Linebreeding to a particular outstanding male may be practiced by a breeder who does not own the male or cannot purchase him. If he can purchase one or more high-quality sons of the admired sire, this would allow the practice of linebreeding to increase the relationship between the young produced and that particular sire.

A word of caution about linebreeding is appropriate. It will be most successful when used by breeders who recognize its potentialities and its limitations and by those who have made a detailed study of the principles of breeding. Even in these instances, success will depend upon the breeder's ability to find and recognize individuals of outstanding merit. Never

theless, we probably could make more use of this system than we have been making in the past few years

Questions and Problems

- 1 Define linebreeding
- 2 Explain the main differences between inbreeding and linebreeding
- 3 What are the main genetic effects of linebreeding?
- 4 Explain why breeders often look upon linebreeding with favor but avoid inbreeding
- 5 Outline a system of linebreeding in which you would linebreed to a male you do not own or is now dead. Explain why you might use this system in preference to others which could be used
- 6 What are some limitations for the use of linebreeding?
- 7 When should linebreeding be used?
- 8 In your opinion, was Prince Domino a carrier of the dwarf gene? Explain why you gave this answer

20

Outbreeding and Crossbreeding

CROSSBREEDING IS THE MATING OF ANIMALS OF TWO OR MORE DIFFERENT BREEDS. Outbreeding is the mating of unrelated animals within a breed. Although crossbreeding is more extreme than outbreeding, the genetic effects of both are similar.

GENOTYPIC AND PHENOTYPIC EFFECTS OF OUTBREEDING AND CROSSBREEDING

The genetic effects of outbreeding and crossbreeding are exactly the opposite of those of inbreeding. Whereas inbreeding tends to make more pairs of genes homozygous, outbreeding and crossbreeding tend to increase heterozygosity for all of the pairs of genes when the parents possess different alleles. For instance, if breed one is homozygous dominant and breed two is homozygous recessive for a particular gene pair, all of the offspring from a cross of animals of these two breeds will be heterozygous. For breeds and lines that are homozygous for a given trait, the maximum amount of heterozygosity is attained in the F_1 . With the segregation of the genes in later generations, heterozygosity diminishes.

These same statements also apply when more than one pair of genes affect a particular trait, so that varying degrees of heterozygosity are expressed, thus we may speak of an animal as being more, or less, heterozygous than another for a particular trait.

Outbred or crossbred animals are less likely to breed true than are inbred animals. This is due to heterozygosity and means that they are less likely to transmit the same genes to all of their offspring. This may be illustrated by the following example. A male of genotype $AABBCCDD$ produces spermatozoa all of which carry genes $ABCD$ to their offspring. A male of genotype $AaBbCcDd$, however, may produce 16 different kinds of spermatozoa with respect to gene combinations and will not breed as

true as the individual that is homozygous for these four gene pairs. Outbreeding and crossbreeding result in an increased uniformity in phenotype within the F_1 generation as far as some of the quantitative traits are concerned because of heterozygosity.

HYBRID VIGOR OR HETEROSIS

Heterosis, or hybrid vigor, is the name given to the increased vigor of the offspring over that of the parents when unrelated individuals are mated. Hybrid vigor includes more than just hardiness. It includes greater viability, a faster growth rate, greater milk producing ability and fertility. This phenomenon has been known for many years. The best known example in animals is the mule, which is noted for its ability to withstand hot weather and hard work. It is the F_1 hybrid resulting from a cross between the male ass and the mare. The offspring of the reciprocal cross, called the hinny or jennet, are also hardy but fewer of such crosses are made because of the scarcity of female asses and because the hybrids are usually smaller than the mule.

The production of hybrid seed corn by developing inbred lines and then crossing them is probably the most important attempt man has made to take advantage of hybrid vigor. Almost all of the corn grown in the corn belt today is grown from hybrid seed, because the yield is greater and the corn is of better quality. In recent years, swine producers have also used crossbreeding to induce hybrid vigor in the commercial production of hogs. This will be discussed in detail in a later chapter.

HOW TO ESTIMATE HETEROSIS FOR ECONOMIC TRAITS

Heterosis is expressed by some traits but not by others. Thus, it is desirable to determine how the degree of heterosis may be estimated for each trait in order to know, in a general way, what traits may be improved by outbreeding and crossbreeding. Heterosis cannot be estimated accurately for a single mating because nongenetic factors may cause a great deal of variation in a particular trait in a single mating. It can be estimated more accurately by comparing groups of crossbred and purebred animals. Animal breeders are not in complete agreement on how this should be done. Some feel that the best measure is the amount that the F_1 exceeds the higher parent. Others feel that heterosis is best measured by comparing the mean of the F_1 offspring with that of the purebred parents, by the following formula:

$$\text{Per cent heterosis} = \frac{\text{Mean of } F_1 \text{ offspring} - \text{Mean of parent breeds}}{\text{Mean of parent breeds}} \times 100$$

For example, suppose that the average litter size at weaning in swine is 7.0 for Breed *A*, 8.0 for Breed *B*, and 8.5 in the F_1 litters. The average litter size in the parent breeds would be 7.0 plus 8.0 or 7.5 pigs. The amount of heterosis would be 8.5 minus 7.5 or 1 divided by 7.5 times 100 or 13.33 per cent.

Estimating the amount of heterosis by comparing the mean of the F_1 offspring with that of the parents seems to be a reasonable method from the genetic standpoint. As was pointed out earlier, one of the characteristics of additive gene action is that the mean of the F_1 individuals coincides exactly with the mean of the parents if environmental variations are not considered. Thus, this kind of gene action is not responsible for heterosis. When nonadditive gene action is important, on the other hand, the mean of the F_1 does not coincide with that of the parents but is either above or below it. In some instances, it may even be higher than the high or lower than the low parent.

GENETIC EXPLANATION OF HETEROSIS

Heterosis is caused by heterozygosity involving genes with nonadditive effects. Nonadditive gene action includes dominance, overdominance, and epistasis. The effects of these three types of action will be discussed separately.

DOMINANCE

The decline in vigor due to inbreeding indicates very strongly that there are many recessive genes in farm animals that have deleterious effects on the vigor of the animal, varying from the lethal to the slightly detrimental. Since there are so many different pairs of genes influencing the expression of quantitative traits, some pure breeds and some inbred lines could be homozygous recessive for some pairs of genes. Many of our breeds in the United States could be homozygous for many genes, or at least, the frequency of one allele may be much higher than that of the other, since they have descended in many cases from a relatively few imported animals. It has been reported that over one-half of the American Shorthorns trace to one bull in their pedigree.² For example, where several pairs of genes control one trait, one breed could be homozygous dominant for several pairs and homozygous recessive for another ($AABBCCdd$), while the second could be, respectively, homozygous recessive and homozygous dominant for those pairs ($aaBBCCDD$). When individuals of the two breeds were crossed, the F_1 ($AaBBCCDd$) would be superior to both parents in that particular trait, having at least one dominant gene in each pair.

TABLE 20

EXAMPLE SHOWING HOW DOMINANCE MAY BE RESPONSIBLE
FOR THE EXPRESSION OF HETEROSIS*Assumptions:*

That environment has no influence on the expression of genes.

That animals of genotypes *AAbb*, *Aabb*, *aaBB*, and *aABb* gain 1.80 pounds per day, those of genotypes *AABB* and *AaBb* gain 2.20 pounds per day, whereas those of genotype *aabb* gain 1.60 pounds per day.

Generation	Genotypes	Phenotypes daily weight gain in pounds	Average daily weight gain in pounds
P_1	<i>AAbb</i>	1.80	1.80
	<i>aaBB</i>	1.80	
F_1	<i>AaBb</i>	2.20	2.20
F_2	1 <i>AABB</i>	2.20	2.01
	2 <i>AABb</i>	2.20	
	1 <i>AAbb</i>	1.80	
	2 <i>AaBB</i>	2.20	
	4 <i>AaBb</i>	2.20	
	2 <i>Aabb</i>	1.80	
	1 <i>aaBB</i>	1.80	
	2 <i>aaBb</i>	1.80	
	1 <i>aabb</i>	1.60	

Data presented in Table 20 illustrate further how dominance is a cause of heterosis. Note that in this example, the mean of the F_1 population exceeds the mean of the two parents. Note also that in the F_2 there is the beginning of a regression toward the mean of the P_1 .

Since dominance is responsible for heterosis, it should be theoretically possible to capture this superiority in a single line by making individuals homozygous dominant for all pairs of genes. For instance, in the example in Table 20, a few of the individuals in the F_2 were *AABB*. If animals of this genotype were mated *inter se*, their offspring would all have this same genotype. However, these homozygous dominants would be difficult to distinguish, for they would resemble the heterozygotes in phenotype. In addition, it is very likely that there are many more than four pairs of genes involved, and these would further complicate efforts to establish homozygous dominance. Thus, even though it is theoretically possible to get a strain that is homozygous dominant for several genes, it is not practical or probable.

OVERDOMINANCE

This type of gene action is also responsible for heterosis. This is illustrated in Table 21, using two different pairs of genes that affect the same trait. In actual practice, several pairs of genes with overdominant action may affect the same trait, but effects of the different pairs may not be equal, some having a greater effect than others.

With this kind of gene action, it would never be possible to fix heterosis in a single pure strain, because the gene action is entirely dependent upon heterozygosity. The only way to take advantage of such kind of gene action would be to first form inbred lines and make them homozygous by inbreeding. Then the lines would have to be tested in crosses to find which lines combine best and induce the most heterosis in their offspring. Once this series of test crosses was made, the best-combining

TABLE 21

EXAMPLE SHOWING HOW OVERDOMINANCE MAY BE RESPONSIBLE FOR THE EXPRESSION OF HETEROSIS

Assumptions:

That environment has no influence on the expression of rate of gain.

That each pair of heterozygous genes has an equal effect on rate of gain

That animals with both pairs of genes homozygous, gain at the rate of 1.60 pounds per day, those with one pair homozygous and one pair heterozygous, at the rate of 1.90 pounds per day; and those with both pairs heterozygous, at the rate of 2.20 pounds per day.

Generation	Genotypes	Phenotypes daily weight gain in pounds	Mean daily weight gain in pounds
P_1	$A^1A^1B^1B^1$	1.60	1.60
	$A^2A^2B^2B^2$	1.60	
F_1	$A^1A^2B^1B^2$	2.20	2.20
F_2	1 $A^1A^1B^1B^1$	1.60	1.90
	2 $A^1A^1B^1B^2$	1.90	
	1 $A^1A^1B^2B^2$	1.60	
	2 $A^1A^2B^1B^1$	1.90	
	4 $A^1A^2B^1B^2$	2.20	
	2 $A^1A^2B^2B^2$	1.90	
	1 $A^2A^2B^1B^1$	1.60	
	2 $A^2A^2B^1B^2$	1.90	
	1 $A^2A^2B^2B^2$	1.60	

TABLE 22

EXAMPLE SHOWING HOW EPISTASIS MAY BE RESONSIBLE FOR THE
EXPRESSION OF HETEROSIS*Assumptions:*

That environment has no influence on the expression of rate of gain.

That individuals of genotypes combining one or more *A* and *B* genes, gain at the rate of 2.00 pounds per day, whereas all other genotypes gain at the rate of 1.60 pounds per day.

Generation	Genotypes	Phenotypes daily weight gain in pounds	Average daily weight gain in pounds
P_1	<i>AABB</i>	2.00	1.80
	<i>aabb</i>	1.60	
F_1	<i>AaBb</i>	2.00	2.00
F_2	1 <i>AABB</i>	2.00	1.83
	2 <i>AABb</i>	2.00	
	1 <i>AAbb</i>	1.60	
	2 <i>AaBB</i>	2.00	
	4 <i>AaBb</i>	2.00	
	2 <i>Aabb</i>	1.60	
	1 <i>aaBB</i>	1.60	
	2 <i>aaBb</i>	1.60	
	1 <i>aabb</i>	1.60	

original parents would have to be crossed again to produce heterozygous individuals. (This is exactly what is done in producing hybrid seed corn.) The fact that this heterosis could not be fixed is obvious in Table 21. If F_1 heterozygotes mated *inter se*, already in the F_2 , by segregation and recombination of genes, the means would regress, and only 4 out of every 16 individuals would retain the induced heterozygosity and heterosis. Further mating among the individuals of succeeding generations would only result in further disruption of the heterozygosity in the population, and an over-all decline in heterosis, and a regression of the mean of the population to the mean of the original parents.

In dominance and overdominance, the heterotic effect is due to the interaction of genes that are alleles, even though several pairs of alleles may affect the same trait. In epistasis the interaction is between pairs of genes that are not alleles. It is theoretically possible to fix heterotic effects that are due to epistasis in a single pure line, as is the case with dominance, but this would also be extremely difficult and may not be probable or practical.

From the foregoing discussion, it becomes very apparent that it is difficult, if not impossible, to fix heterosis, that is, to attempt to maintain heterosis by mating those individuals having the highest degree of heterosis. The most practical procedure of making use of heterosis seems to be the formation of distinct lines or breeds and then crossing them to find those which give the greatest hybrid vigor. Such a procedure will work regardless of the kind of nonadditive gene action that is responsible for the heterosis.

ADDITIVE GENE ACTION

This kind of gene action is not responsible for heterosis, since the average of the F_1 would coincide with the average of the two parents. This is illustrated in Table 23.

WHAT DETERMINES THE DEGREE OF HETEROSIS?

Not all traits in farm animals are affected to the same degree by heterosis. Those traits which are expressed early in life, such as survival and growth rate to weaning, seem to be affected the most, whereas feed lot performance, as measured by rate and efficiency of gain after weaning, is only moderately affected. In general, heterosis seems to have very little influence on carcass quality in farm animals. It may be pointed out again that those traits which show the greatest degree of heterosis are the same ones which show the greatest adverse effects when inbreeding is practiced.

Traits which are highly heritable seem to be affected very little by heterosis, whereas those which are lowly heritable are affected to a greater degree. A good example of this phenomenon is fertility or litter size in swine. This trait is only about 15 to 17 per cent heritable but is affected greatly by hybrid vigor.

Evidence also indicates that the degree of heterosis depends upon the degree of genetic diversity of the parents that are crossed. Thus, a higher degree of heterosis should be obtained when different breeds are crossed than when lines within the same breed are crossed. Furthermore, crossing breeds having greater differences in their genetic backgrounds should give more heterosis than crossing breeds having similar genetic backgrounds. This is reasonable from a theoretical standpoint. Unrelated par-

TABLE 23

EXAMPLE SHOWING HOW ADDITIVE GENE ACTION IS NOT RESPONSIBLE FOR THE EXPRESSION OF HETEROSIS

Assumptions:

That environment does not influence the expression of rate of gain.

That the residual genotype of *aabb* gains at the rate of 1.60 pounds per day, and the plus or contributing genes *A* or *B* each add .20 pounds to the daily rate of gain.

Generation	Genotypes	Phenotypes daily weight gain in pounds	Average daily weight gain in pounds
P_1	<i>AABB</i>	2.40	2.00
	<i>aabb</i>	1.60	
F_1	<i>AaBb</i>	2.00	2.00
F_2	1 <i>AABB</i>	2.40	2.00
	2 <i>AABb</i>	2.20	
	1 <i>AAbb</i>	2.00	
	2 <i>AaBB</i>	2.20	
	4 <i>AaBb</i>	2.00	
	2 <i>Aabb</i>	1.80	
	1 <i>aaBB</i>	2.00	
	2 <i>aaBb</i>	1.80	
	1 <i>aabb</i>	1.60	

ents are less likely than related parents to be homozygous for the same pairs of genes. This is because the original stocks of the unrelated parents differed in their gene complements; or, if the unrelated parents are descendants of the same original stock, segregation and recombination of genes has caused their relationship to become more remote. For example, if individuals of genotype *aaBBCCdd* were crossed, the F_1 would not be superior to the parents because of heterosis, regardless of the kind of nonadditive gene action involved. On the other hand, if individuals of that genotype were crossed with individuals of genotype *AAbbccDD*, heterosis would be expressed in the F_1 if nonadditive gene action were important. In summary, then, we can say that heterosis depends upon nonadditive gene action and upon one parent being homozygous for one allele in which the other parent is homozygous for the other.

PHYSIOLOGICAL BASIS OF HETEROSIS

Very few investigations have been made to determine the physiological basis of heterosis in farm animals. Gregory and Dickerson¹ made com-

parisons of inbred and topcross pigs (those from the mating of inbred boars to outbred sows) on the same level of feed intake. They found that topcross pigs required 10 per cent less feed per unit of gain, made 10 per cent faster gains and possessed less fat and more muscle and bone at a market weight of approximately 200 pounds. These advantages occurred even though there was no significant difference in the ability of inbred and topcross pigs to digest their food. This led to the conclusion that the topcross pigs had a more efficient metabolic system, which could have been due to a lower maintenance requirement or less energy loss during the growing fattening period.

PRACTICAL USES OF CROSSBREEDING

Crossbreeding is used by the producer of market animals. It is used mainly in an effort to maintain heterosis which cannot be fixed within a pure line or breed. Crossbreeding is used widely for the production of market hogs in the corn belt, and for the production of beef cattle in the Southern and Southwestern region of the United States. The uses and advantages of this system of mating will be discussed for each species of farm animals in later chapters.

Crossbreeding has also been used in recent years to establish a broad genetic basis for the development of a new breed. The initial crossbreeding is then followed by inbreeding and selection for the characteristics desired in the new breed. An example of this system is the development of the Santa Gertrudis breed of cattle by the King Ranch in Texas from a Shorthorn \times Brahman cross. Other examples are the development of several new breeds of swine. These will be discussed in more detail in a later chapter. Fundamentally, the procedure has merit, because no one breed of farm animals possesses all favorable or desirable genes.

Many breeders object to the use of crossbreeding for various reasons. One reputed disadvantage of crossbreeding is that the offspring lack uniformity of coat color. This objection is more likely to be valid where three or more breeds are used in a crossbreeding program. Some breeders have overcome this difficulty by developing inbred lines all of the same color. As mentioned earlier in this chapter, crossbred animals may be more uniform for some of the economic traits such as litter size and weight at weaning than purebred or inbred animals. Lack of uniformity in unimportant traits should not be considered a fundamental disadvantage of the crossbreeding system of mating.

PRACTICAL USE OF OUTBREEDING

Outbreeding is the system of mating used most widely by purebreeders in the production of purebreds at the present time. It is practiced to off

set the adverse effects accompanying inbreeding. Also, many breeders feel they can purchase from other breeders males of higher quality than they can produce in their own herds. One contributing factor to the widespread use of outbred sires has been the extreme importance that has been placed on show-ring winnings. The breeders feel that they must obtain a certain amount of advertising for their own herds by purchasing progeny of grand champion sires. This does increase the chances of bringing more desirable show-ring type into the herd, but the chief advantage is that a well-known name thereby appears on one side of the pedigree of the young stock they have for sale. This has resulted in more attention being paid to names than to merit in many instances.

OTHER SYSTEMS OF OUTBREEDING

Other systems of outbreeding are grading and topcrossing. In grading, purebred males of superior merit are mated to grade females or females of low quality. This system has been used considerably in the past, especially in the West where purebred Hereford bulls were used on Longhorn and grade cows. It has also been used extensively where tested purebred dairy bulls have been used by artificial insemination in grade herds.

One of the features of grading is that the greatest improvement is usually made with the first cross, with less and less improvement made in later generations as the level of quality in the herd increases. Some of the improvement made in the first cross is due to heterosis; in later generations the level of heterosis tends to regress. The factor that could be responsible for continued improvement when grading is practiced is the introduction of desirable additive genes with plus effects into a herd which originally lacked them. Then, selection for higher quality in succeeding generations maintains the genes in the breeding stock. This should be especially true for traits that are highly heritable. Intensive selection must be practiced, however, if these traits are to be continuously improved.

Until recently, topcrossing was practiced in the production of purebred animals. Topcrossing refers to the last male in the top side of the pedigree and derives its name from this fact. An example is "Scotch-topped Shorthorns," which means that the dam was a regular Shorthorn but the sire was of straight Scotch breeding. More recently topcrossing has been used to refer to the mating of inbred males with unrelated females. If the females belong to the same breed as the inbred male, this is, of course, a form of outbreeding. However, if the females to which the inbred male is mated belong to a different breed this is a form of crossbreeding. Usually, no attempt is made to distinguish between topcrossing that is outbreeding or crossbreeding.

References

1. GREGORY, K. E., and G. E. DICKERSON. "Influence of Heterosis and Plane of Nutrition on Rate and Economy of Gains, Digestion and Carcass Composition of Pigs," *MoAESRB* 493, 1952
2. WING, J. M., and C. J. WILCOX. "Inbreeding—Friend or Foe?" Contribution from the Purebred Dairy Cattle Association Research Committee, Box 150, Peterborough, New Hampshire, 1960.

Questions and Problems

1. Define outbreeding and crossbreeding.
2. What are the genotypic and phenotypic effects of outbreeding?
3. Define heterosis and give examples where it has been used to advantage in farming operations.
4. Parents from two different breeds of swine were used for crossbreeding purposes. Litter size in one breed averaged 6.6 pigs at weaning and 8.0 in the other. In crossbred gilts saved from these litters for breeding purposes, litter size at weaning averaged 9.30 pigs per litter. What is the percentage of heterosis in this example?
5. What kinds of gene action are responsible for heterosis and what type is not?
6. What traits in farm animals seem to be affected the most by heterosis?
7. What seems to determine the degree or amount of heterosis obtained through crossbreeding?
8. Outline in detail the procedure to follow in using heterosis to the greatest possible extent in farm animals.
9. What appears to be the physiological cause, or causes, of heterosis in farm animals?
10. What are the main uses of crossbreeding?
11. Define grading and topcrossing.
12. What is the main advantage of crossbreeding in farm animals and how may this be used? What is the main disadvantage?

21

Summary of Animal Breeding Principles

IN THE PRECEDING CHAPTERS WE DIS-
cussed in detail the principles involved in animal breeding. Before showing how they may be applied to the improvement of the various species of farm animals we shall summarize and restate these principles.

SAMPLING NATURE OF INHERITANCE

The inheritance of individuals is transmitted from parents to offspring by means of genes located on the various chromosomes. There are hundreds and probably thousands of genes, and they occur in pairs except those on the nonhomologous parts of the *X* and the *Y* chromosomes. Of each pair of genes, the individual receives one from the mother and one from the father; and to each of his offspring the individual will give one member of the pair. Thus, for every pair of genes, each offspring receives a sample one-half of its inheritance from each parent. Since there are many pairs of genes, and some are in the homozygous and some in the heterozygous state in the individual, the samples may be quite different for any two.

ROLE OF THE ANIMAL BREEDER

Differences in genes, or variations in individuals due to differences in genes, is the raw material with which the animal breeder must work. The animal breeder cannot create new genes, but must work with the genetic variation that already exists in his animals.

Genetic variation is the result of mutations of genes which have occurred during the production of many, many new generations of animals.

These mutations, along with selection, have made some animals more suitable for a particular purpose or a particular environment

The animal breeder today is more interested than ever in producing animals that are highly efficient for a particular purpose. The dairy cattle breeder is interested in developing a herd that gives the largest amount of milk per animal for the smallest amount of feed consumed. The beef producer is interested in the efficiency of beef production, but recently he has been giving increased attention to carcass quality. In other words, the problem now is not to develop new and better breeds, but to improve existing ones or to combine them in a way as to take advantage of heterosis. Of course, some new breeds have been developed from cross bred foundations, but their superiority to the more popular older breeds has still to be proved. There seems to be some potential for the development of new and superior breeds from a crossbred foundation if the two or more parent breeds possess different desirable genes.

The role of the animal breeder is to identify those animals that possess desirable genes or combinations of genes and to concentrate in his herd as many of these genes as possible. In attempting to find superior animals, he is often confused by environmental effects and by the different modes of gene action and interaction. He should compare prospective breeding animals in as like environments as possible, preferably in one similar to that in which their offspring would be raised, and he should compare animals near the age at which he would market the offspring. He must choose superior individuals on the basis of information in pedigrees, the individuality of the prospective breeding animals, and on information on collateral relatives and progeny when their records are available. His breeding program will be effective if the traits to be selected for have been measured accurately and if they are highly heritable, indicating that additive gene action is the cause of most of the genetic variation. If non additive gene action is the most important genetic influence on the traits he plans to select for, his breeding program will have to include the development of inbred lines first. Then these will have to be tested in crosses to identify those with the superior combining ability in order to take advantage of nicking effects or heterosis.

INFORMATION NEEDED TO FORMULATE EFFECTIVE MATING AND SELECTION SYSTEMS

When developing a breeding program the breeder must first decide what traits are the most important to select for from the economic standpoint. His decision will depend upon the species of farm animals with which he is working, the feeding program he intends to use, the kind of product he intends to market, and the sale price of that product. In most cases, the breeder will limit the number of traits selected for and will

include these traits in an index. The amount of weight he gives each trait in the index will depend upon the heritability of that trait, its relative economic value, and the genetic correlation of that trait with others of economic importance. Example index formulas will be given for each class or species of farm animals in later chapters.

Next he must acquaint himself with the methods that have been devised to make accurate measurements and records; thereby, the breeder can distinguish more satisfactorily between genetic and environmental effects both in prospective breeding animals and in generations during the breeding program. Actual measurements of such traits as weight, milk production, or percentage of lean cuts should be made and not estimated. The use of correction factors to adjust records of all animals in the herd to a comparable age, to the same-age-of dam basis, for sex, and other variables, whenever applicable, enables the breeder to make comparisons more accurately. His accuracy in choosing genetically superior animals for breeding purposes and in evaluating the progress of his breeding program will be increased if he keeps detailed written records.

Another fact the breeder needs to know in planning his program is which kind of gene action, additive or nonadditive, has the greater influence on each of the important economic traits. Additive gene action is indicated when the heritability of the trait is high, as measured by the resemblance between parents and their offspring, and when the crossing of breeds results in an average of the F_1 that closely approximates the average of the parents. Additive gene action is also indicated, but not yet proven, when sex differences for a trait are large. When additive gene action has more influence, mass selection (mating the best to the best) will be effective. Nonadditive gene action is indicated when the heritability of a trait is low, when inbreeding has had detrimental effects, and when outbreeding or crossbreeding has had beneficial effects. Nonadditive gene action is also indicated when the average of the F_1 individuals differs from the average of the two parental groups (heterosis). When nonadditive gene action has more influence on a trait, the greatest improvement in performance will come from the crossing of strains or lines known to have good nicking or combining ability. The breeder may want to breed and select for several different traits of which some are affected by additive and some by nonadditive gene action. The recommended procedure here would be to form pure lines or breeds by selection for improvement in those traits that are highly heritable; then, to cross these lines or breeds to improve those traits that show heterosis.

The breeder should also know whether genetic correlations are important among the different traits selected for and whether the correlations are positive or negative. Some information is available for the important traits, and these will be discussed in the chapters dealing with each of the species of farm animals.

The breeder can make more effective plans if he also can determine whether or not genetic-environmental interactions influence the traits he wishes to select for. As discussed earlier today's breeder has little information about this factor, but further research should provide more.

WHEN TO USE INBREEDING AND LINEBREEDING

Inbreeding and linebreeding are practiced to produce seed stock. Intensive inbreeding is done, as a general rule, with the intention of using inbred animals for crossing purposes.

If this is not the breeder's main objective, intensive inbreeding might not be desirable, for the main phenotypic effect of inbreeding and linebreeding is a decline in the performance traits that are affected greatly by nonadditive gene action. Much of this decline must be due to the fact that detrimental recessive genes are revealed by increased homozygosity. In general, the traits affected most by inbreeding are those associated with physical fitness. The decline in performance in these traits seems to be greater in some inbred lines than in others, but in general, the decline occurs in spite of selection against it.

The producer of seed stock, himself, must be prepared to accept a certain amount of decline in performance of his stock and must expect the appearance of some inherited defects. He must decide whether or not the expected increase in prepotency or uniformity of genetic composition will overbalance the decline in performance.

If inbreeding is practiced for some other purpose than the production of seed stock to be used in crosses, such as the production of purebreds for show-ring purposes, the degree of inbreeding should be held to a minimum and should be increased slowly, with intensive culling and selection of breeding animals that reproduce that line. These methods of breeding should not be used by the commercial livestock producer, who is an animal multiplier and not a producer of seed stock. His purpose is to produce the greatest amount of salable product per breeding animal, and a lowered productivity of the breeding animals will not accomplish this.

Inbreeding and linebreeding should not be used in herds made up of average or mediocre breeding stock, for several undesirable recessive genes may be present and frequently will be brought together and appear phenotypically, this may result in the discarding of the whole inbred line sooner or later.

The building of superior inbred lines of livestock is a slow, time-consuming, and methodical process and probably should be undertaken only by the breeder who has the knowledge, the time, and the necessary capital to continue the process to its completion.

WHEN TO USE OUTBREEDING AND CROSSBREEDING

Outbreeding is the form of mating most often used by present-day purebred breeders in the production of purebreds. It will probably continue to be widely used, because, by mating females in his herd or flock to nonrelated males the breeder avoids the effect of inbreeding. In outbreeding, the breeder must attempt to purchase the best genetic material he can find at a price he can afford to pay, and he must always try to find a male that is superior to the females in his herd. Recently, breeders have been selecting males on the basis of both type and performance rather than on type alone. The use of superior males proved by performance tests should improve the over-all performance of the herd and produce superior seed stock to sell to the commercial livestock producers.

The purebred breeder should purchase older males that have been progeny-tested and proved of superior genetic worth. Often the older male of outstanding breeding ability is sold because he has so many daughters in the herd that the owner would be forced to use inbreeding if he were retained in the herd. Superior genotypes of this kind should be used in someone's herd as long as the animal remains fertile, in order to improve the over-all production of a herd and possibly a breed.

Crossbreeding is the mating system that should be used by the livestock multiplier or the commercial livestock producer. The class of livestock may be important, however; crossbreeding is useful in swine, but may not be in dairy cattle. Crossbreeding effects are the opposite of inbreeding and linebreeding effects in that traits associated with physical fitness are improved; but the breeding worth of the individuals may be lessened to a certain degree because they are heterozygous and do not breed as uniformly true as inbred animals.

Some livestock producers become so enthusiastic about crossbreeding that they may forget that some traits in farm animals do not show heterosis. Thus, it is important for the breeder to be familiar with which traits show heterosis and which ones do not. These will be discussed in detail for each species of farm animals in later chapters.

In conclusion, it is well to emphasize that, for the greatest improvement in livestock breeding, the breeder must not only be familiar with the raw material and the tools available to mold this raw material, but he must also know how to use both to the greatest advantage.

22

Systems of Breeding and Selection in Swine

SWINE ARE KNOWN AS 'MORTGAGE lifters' and they are reared in large numbers on farms in the Corn Belt region. The past few years have seen a definite change from the lard type to the meat type hog because of the surplus of lard on the market caused by the substitution of vegetable oils for lard for cooking purposes and of detergents for soaps made from lard. Another factor has been the consumer demand for leaner pork. This demand is also a result of growing calorie consciousness. Slim and trim figures have become more desirable and seem to be conducive to longer life and better health.

Swine breeders no longer select breeding animals on type alone. Results of swine breeding research have impressed on breeders the importance of selection for performance as well as for type. The fact that breeders are now more interested in systematic selection and breeding practices is demonstrated by the number of swine-evaluation stations that have been established in the United States during the past few years.

Swine breeding research has yielded many practical results that are now being used by swine breeders. Much more research work still needs to be done, however, especially in the determination of genetic correlations between traits, in possible genetic-environmental interactions, and in improved methods of selecting and breeding for superior performance. This chapter will be devoted to a discussion of selection and breeding methods now recommended on the basis of research in swine breeding.

TRAITS OF ECONOMIC IMPORTANCE AND HOW TO MEASURE THEM

Only those traits which are the most important from the economic standpoint should be considered in a breeding program. Selection for

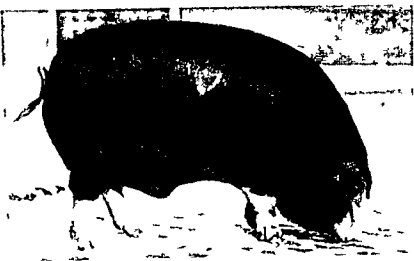


FIGURE 49 GRAND CHAMPION BARROW AT THE INTERNATIONAL LIVESTOCK SHOW IN 1919 CONSUMERS NOW DEMAND MORE LEAN AND LESS FAT IN PORK PRODUCTS (COURTESY OF THE UNIVERSITY OF MISSOURI)

many different traits, of which some are of minor importance, such as color patterns, will result in less selection pressure being applied for those traits which are most important. For this reason, the discussion here will be limited to only the most important traits.

TOTAL LITTER WEIGHT AT WEANING

Litter weight at weaning is a measurement of net merit for preweaning performance in swine. It gives a measurement of the fertility of the sow, because the heavier litters at weaning are usually the larger litters. It also is an indication of the milking and mothering ability of the sow and the vigor and growth rate of the pigs. Litter size and weight at weaning are determined by the number of pigs born per litter and the ability of these pigs to survive to weaning. To wean a litter of 10 pigs, sows must farrow at least 10, and in most cases one or two more. On the other hand, large litters at birth are not advantageous if the sow is a poor mother and

FIGURE 50 LARGE LITTERS AT WEANING ARE NECESSARY FOR A PROFIT IN PORK PRODUCTION. THIS IS A LITTER IN WHICH EIGHTEEN PIGS WERE BORN AND SIXTEEN WEANED WITH A TOTAL 56-DAY LITTER WEIGHT OF 687 POUNDS (COURTESY AMERICAN LAND-RACE ASSOCIATION)

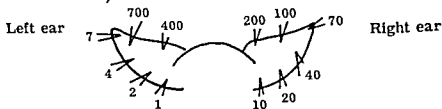


crushes many of her pigs during their first few days of life, or if the pigs are born so weak that they fail to survive to weaning. Much of this trouble can be prevented by proper feeding and management of the sows and litters, but gene actions of various types are known to affect these traits.

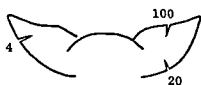
To measure litter size and weight at weaning accurately, it is necessary to identify each litter, and preferably each pig, at birth, by using an ear-marking system or by tattooing a number in the pig's ear. Many ear-marking systems have been proposed by breed associations and by experiment stations, all of which are satisfactory. The ear-notching system shown in Figure 51 may be used to identify several thousand individual pigs by litter number and individual number.

In the past, most pigs have been weaned at 56 days, but since the advent of sow milk replacers and higher quality creep rations, many pigs are being weaned at from three to five weeks of age. The age at weaning will depend upon the wishes of the swine breeder, his facilities, and the farrowing system he is following. For selection purposes within a herd, however, all pigs should be weaned at the same age, so litters may be compared on the same age basis. Often it is not possible to weigh all litters as they reach an exact age. Correction factors have been calculated to adjust litter weights to a 56 day basis. The one given in Table 24 may be used for this purpose. To use these correction factors, let us suppose that pigs were weighed at 61 days of age instead of 56. The weight is

FIGURE 51 THIS SYSTEM OF EAR MARKING MAKES IT POSSIBLE TO GIVE EACH PIG A SPECIFIC NUMBER. THOUSANDS OF PIGS CAN BE MARKED BY THIS SYSTEM WITHOUT DUPLICATION. (FROM MISSOURI AGRICULTURAL EXPERIMENT STATION RESEARCH BULLETIN 587.)



Position value of ear notches



Pig No. 124



Pig No. 784

TABLE 24

CORRECTION FACTORS FOR ADJUSTING LITTER WEIGHTS OF PIGS TO A 56-DAY BASIS

<i>Age when weighed (days)</i>	<i>Multiply total litter weight by this factor to adjust to 56 days</i>
50	1 1801
51	1 1471
52	1 1154
53	1 0849
54	1 0555
55	1 0272
56	1 0000
57	9738
58	9485
59	9241
60	9006
61	8779
62	8560
63	8359

adjusted by multiplying the weight of the litter at 61 days by the correction factor (0.8779) given in Table 24

WEIGHT AT 154 DAYS OF AGE

The weight of each pig at 154 days of age is another important economic trait. A weight taken at this time is actually a total measurement of all gains made from birth. If 56-day weights for each pig are available, the rate of gain from weaning to 154 days of age can be calculated by dividing the weight gained by 98. Since it is not always possible to weigh each pig or each litter at exactly 154 days of age, correction factors have been devised to adjust the weights to this standard age basis.²⁸ The following has been suggested for this purpose:

$$\text{Adjusted weight} = \frac{(\text{Actual Weight} + 154)}{\text{Actual Age} + 45} (199) - 154$$

Other breeders prefer to record the average daily gain from shortly after weaning to a market weight of 200 pounds. As a general rule, no correction is made for the age of the pig, but the numbers of pounds gained divided by the total days on feed gives an average daily gain figure.

Postweaning gains are easy to calculate for each pig, whether a standard 154-day weight or the average daily gain from weaning to market weight.

is used. For accuracy of records, it is to be emphasized that pigs fed in groups or in litters must bear individual identification numbers.

ECONOMY OF GAINS FROM WEANING TO MARKET WEIGHT

The economy of gains is also of considerable importance in pork production. The amount of feed required per pound of gain by individuals is difficult to calculate, however, because it requires individual feeding, which is expensive and impractical. Individual feeding is usually practiced only for boars, because a boar is the most important single individual in the herd; he supplies one-half of the inheritance for many litters, during a season whereas each sow supplies the inheritance for only one. In addition, fewer boars are required for breeding purposes, and only the top herd sire prospects need to be individually fed.

Estimates of the feed efficiency for a pig may be obtained by feeding an entire litter together in one pen or by feeding two barrows (or boars) and two females together from weaning to market weight. This gives a figure for each litter and thereby an estimate for each member of the litter. Feeding pigs in this manner is less expensive than individual feeding, but still is not practical enough to be used by many breeders. It is being used to a considerable extent by swine-evaluation stations now in operation in the United States.

All pigs within a herd should be compared on as nearly the same basis as possible for efficiency of gains by starting them on feed at about the same weight and taking them off the gain test at the same final weight. This is necessary because a pig requires more feed per pound of gain

TABLE 25

THE VARIATION IN PERFORMANCE OF DUROC BOARS FED IN INDIVIDUAL PENS FROM WEANING TO 200 POUNDS LIVE WEIGHT

No of boar	Avg daily gain (lbs)	Lbs feed consumed per day	Lbs feed per pound gain
104	2.03	7.51	3.70
105	1.96	7.54	3.85
148	2.14	7.94	3.70
157	2.05	7.51	3.67
207	1.89	7.49	3.97
209	2.03	7.67	3.78
209-1	1.76	6.96	3.96
236	1.81	7.06	3.89
238	1.94	6.99	3.61
276	1.86	6.67	3.59
355	2.17	7.48	3.43
500	1.66	6.69	4.03

between 100 and 200 pounds than between 50 and 100 pounds. For this reason, the beginning and ending weight for all of the pigs is held as constant as possible in measuring the economy of gains.

Pigs to be compared for efficiency of gains must all be fed the same rations. Less pounds of feed per unit of gain will be required with concentrated, high-energy rations than with bulky, less-concentrated rations. Different herds do not all get the same kind of rations, and for this reason, it is difficult to compare their economy-of-gain figures where management feeding practices may vary widely also, making comparisons difficult. Another consideration is that, unless self-feeders are adjusted very carefully, feed wastage may be considerable, and the resultant economy-of-gain figures may be inaccurate.

TYPE AND CONFORMATION SCORE AT MARKET WEIGHT

Different views may be expressed on the value of calculating type and conformation scores of pigs at market weight. Until the last few years, most of the emphasis in swine production and selection was on show ring type. More recently, however, type and conformation have been emphasized less and preference has been given to the percentage of lean cuts whenever possible. Nevertheless, there is a certain amount of correlation between meatiness and scores for meat type. Thus, this trait should be given consideration by purebred breeders.

Many complicated score cards have been used in the past, but probably they are of no more value than a simple scoring system in which the animals are scored A, B, C, D, and E, with A being the most desirable and E the least desirable. Scores of this kind are more valuable when a committee of three or more judges do the scoring and an average is recorded for each pig.

CARCASS DESIRABILITY

More and more attention is now being paid by breeders to carcass desirability in swine, mainly because of the demand for more lean and less fat in pork products. Formerly, carcass desirability could be determined only after slaughter, but in recent years attempts have been made to measure carcass quality in the live animal before slaughter. One of the most useful methods developed is the measurement of backfat thickness in the live animal by using a scalpel to cut the skin and then thrusting a ruler (or a ruled probe) into the fat until it is stopped by contact with the muscle fibers of the body.¹⁶ Measurement of backfat thickness in the live hog by this method is as accurate in most instances as measurement of backfat taken in the carcass, and has been a valuable criterion in selecting breeding stock.

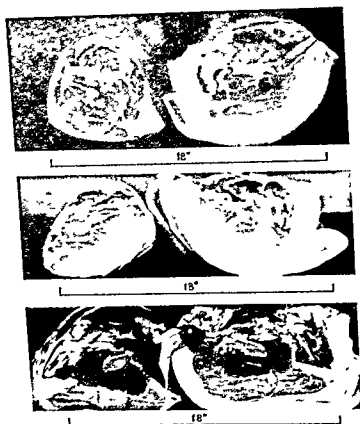


FIGURE 52 DEFINITE DIFFERENCES IN MEATINESS IN SWINE SHOW UP AFTER SLAUGHTER. THESE WERE FROM THE SAME HERD IN THE SAME YEAR. (COURTESY OF THE UNIVERSITY OF MISSOURI.)

Other methods of estimating the amount of lean and fat in the live animal are determination of the level of creatinine in the blood and urine, blood lipids, blood volume, and changes in the leucocyte numbers at the end of the fattening period. None of these has proved to be accurate enough for selection purposes, but continued studies may develop methods of greater value. The use of machines utilizing the principle of high-frequency sound which gives a different reading in contact with fat than it does in contact with lean offers promise in this respect and is being tested in many places.

Carcass data on littermates of breeding animals have been used for selection purposes. This method of selection has been used in Denmark for many years in the development of bacon qualities in the Landrace breed. It is now being used in many other countries, and in the United States, many of the breed associations have initiated the Meat Hog Certification programs in which a barrow and a gilt from a litter are used to obtain carcass data to certify the litter. Certification of the litters is dependent upon the length of body, backfat thickness, and area of the loin-eye muscle at certain weights. Litters that qualify must also meet certain age standards at slaughter and must be from a production-registry litter.

Carcass data obtained in swine-evaluation stations include body-length measurements, backfat thickness, area of the loin-eye muscle and the per-

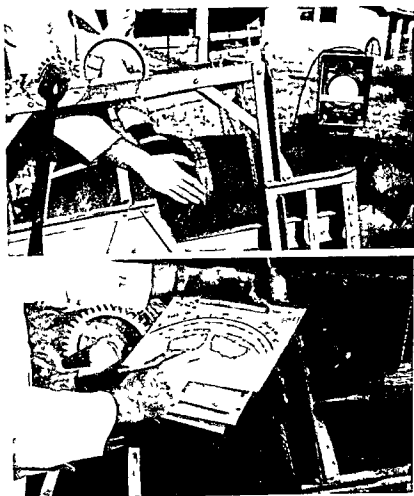


FIGURE 53 LOIN EYE AREA IN THE LIVE HOG MAY BE ESTIMATED THROUGH THE USE OF A SONORAY MACHINE. (COURTESY OF THE UNIVERSITY OF MISSOURI.)

centage of lean cuts. These criteria are used to identify those strains or individuals that possess inherent meat type and other desirable performance qualities so they may be used to produce their kind in an attempt to raise the genetic worth of the entire population.

HERITABILITY OF ECONOMIC TRAITS IN SWINE

Many heritability estimates have been calculated for the different traits, including conformation, performance characters, and carcass quality. A summary of these heritability estimates is presented in Table 26.

Litter size and weight at weaning are lowly heritable, with an average estimate from many studies of approximately 17 per cent. The weight of pigs at 154 days is approximately 30 per cent heritable, whereas growth rate from weaning to 180 to 200 pounds is 29 per cent heritable. Efficiency of gain is about 31 per cent heritable and is high enough to indicate that this trait is affected by additive gene action and that some progress could be made in selection for its improvement. Undoubtedly, if more accurate methods of measuring economy of gain could be developed in which feed wastage was less, the heritability of this trait would be higher.

TABLE 26

HERITABILITY ESTIMATES FOR CERTAIN TRAITS IN SWINE*

	<i>Approx. Average</i>
<i>Items of conformation.</i>	
Length of body	59
Length of legs	65
Number of vertebrae	74
Number of nipples	59
Type	38
<i>Performance characters</i>	
Number of pigs farrowed	15
Number of pigs weaned	12
Weight of litter at weaning	17
Weight of pig at approximately 5-6 months	30
Growth rate (weaning to 180-200 lbs)	29
Economy of gain	31
<i>Items of carcasses</i>	
Length	59
Loin-eye area	48
Thickness of backfat	49
Thickness of belly	52
Per cent of ham (based on carcass wt)	58
Per cent of shoulder (based on carcass wt)	47
Per cent of fat cuts (based on carcass wt)	63
Per cent of lean cuts (based on carcass wt)	31
Carcass score	46

*Mostly after Craft¹

SELECTION INDEXES FOR SWINE

Breeders are seldom interested in selection for the improvement of a single trait. Usually they are interested in improving several traits of the greatest economic importance. A selection index may be used for this purpose. The following index¹² may be used when selecting for sow performance

$$\text{Index} = 2 \left(N_b + 2N_w + \frac{2T_w}{30} \right),$$

where

 N_b = number of pigs born, N_w = number of pigs weaned, and T_w = total litter weight at weaning

For example, if a sow farrowed 10 pigs and weaned eight with a total litter weight of 320 pounds at weaning, her index would be

$$2 \left(10 + 2 \times 8 + \frac{640}{30} \right), \text{ or } 94.6.$$

Another index for selecting pigs on the farm³ is:

$$\text{Index} = -0.5X_1 + 7X_2 - 0.02X_3 + 0.5X_4,$$

where

- X_1 = number of pigs farrowed in the litter,
- X_2 = number of pigs per litter at 154 days,
- X_3 = litter weight at 154 days, and
- X_4 = individual pig weight at 154 days.

Swine-testing stations all over the United States are using indexes for comparing pigs on feeding tests. The index used varies with different stations. The following is an example of one that could be used:

$$\text{Index} = 500 + 30G - 100F - E,$$

where

- G is the average daily gain in pounds,
- F is backfat thickness in inches, and
- E is feed efficiency in pounds of feed required to produce 100 pounds of gain.

The index for a pig that gained 2.00 pounds per day on 280 pounds of feed per 100 pounds of gain and had 1.20 inches of backfat at 200 pounds would be $500 + 30(2.00) - 100(1.20) - 280$, or 160.

The index for each individual in a herd should be calculated and those animals with the highest index kept for breeding purposes. If type or conformation were given consideration, those individuals of the poorest type could be culled and the remainder compared on the basis of the index.

SELECTION EXPERIMENTS WITH SWINE

The amount of progress expected from selection for the various economic traits may be calculated from the selection differentials, heritability estimates for these traits, and the generation interval. The real proof of progress in selection for these traits, however, depends upon results obtained in actual selection experiments.

A cooperative study was made of the amount and effectiveness of selection practiced during the development of inbred lines of swine at several cooperating experiment stations in the Regional Swine Breeding Laboratory.¹² Data used to measure the amount of selection was obtained on 4,521 litters from 38 lines during the period from 1932 to 1948. After adjusting for the expected detrimental effects of increased inbreeding, the average results indicated that selection practiced in the development of mildly inbred lines failed to improve measurably the genetic merit of the lines. One conclusion was that the effectiveness of artificial selection might have been reduced because most of the selection practiced for litter size actually was automatic. That is, this much selection would have occurred if a random sample of the pigs weaned had been chosen for breeding purposes.

A selection experiment was conducted at the Illinois Agricultural Experiment Station for rate of gain.^{20, 1} The experiment involved selection for fast rate of gain in one line of Hampshire pigs and for slow rate of gain in another. At the end of eight to nine generations, there was a difference of 61.8 pounds in the 180-day weights of pigs in the two lines. The results indicated that selection for rate of gain was effective.

The Washington Agricultural Experiment Station conducted an experiment to determine if selection for growth rate is as effective when swine are fed on a low plane of nutrition as when they are full fed.¹⁴ A crossbred foundation stock of Danish Landrace \times Chester White pigs was used, and two lines were formed. One line was full fed from weaning to 150 pounds, then limited fed from 150 pounds to parturition, and then full fed again during lactation. The other line received 70 per cent as much food as the full fed group for each of these periods. Selections were made on the basis of an index including litter size at farrowing and weaning and average daily gain from weaning to 150 lbs. Selection for rate of gain was effective in both lines, the progress made being very close to that expected from the selection differentials and the heritability estimates. When pigs from the two lines were exchanged after the sixth generation of selection, the pigs from the limited fed line made faster gains than those selected for fast gains on a full feed, whereas when both lines were fed on a limited ration, the pigs selected for rapid gains on the limited ration made the faster gains. Thus, a definite genetic-environmental interaction was observed. It was concluded that the results of this experiment supported the contention that breeding animals should be produced and selected in the same environment in which their progeny will be produced.

A selection experiment was conducted at the Alabama Agricultural Experiment Station¹¹ for efficiency of gains in Duroc swine. Two different lines were established from the same foundation stock, with selection for high feed requirements in one line and low feed requirements in another.

This was the only trait considered in the selection experiment. All pigs from each litter were full-fed a mixed ration in individual pens with concrete floors from 72 days of age to a live weight of 225 pounds. At the end of five generations of selection, 67 pigs from the efficient line had required an average of 352 pounds of feed per 100 pounds of gain, whereas 22 pigs from the inefficient line had required an average of 377 pounds, or a difference of 25 pounds.

An experiment designed to study the effects of selection for a single character, backfat thickness in swine, was started at Beltsville in 1954 in Yorkshires and in Durocs. The experiment was designed to select for a line low in fatness and one high in fatness, with a third group as an unselected control.¹⁹ Preliminary results indicate that selection for thinner backfat is effective, although final results have not been published.

SELECTION FOR SWINE IMPROVEMENT IN DENMARK

Denmark has exported most of its surplus of pigs in the form of bacon to Great Britain for more than 50 years,²¹ and the Danish breeding policy has been concentrated toward producing a type of pig to meet this demand for quality. In the 1890's, the Danes started the development of a superior breeding system; it has been used ever since without a change of the general principles, although some changes and improvement have been made occasionally in feeding and handling the pigs.

Special State Recognized Breeding Centers were established for both Landrace and Large Whites in order to supply commercial producers with purebred breeding stock for crossing and to improve the Landrace by selection for carcass quality. The first breeding centers were established in 1895. By 1938, the number of Landrace breeding centers had increased to approximately 250; in 1956 there were 254. The number of Large White centers reached 33 in 1933, but then decreased rapidly, leaving only two breeding centers for this breed in 1956.

It soon became apparent to the Danes that an external examination of pigs was not sufficient to bring about improvement in carcass quality, so this was supplemented by a slaughter test. The first permanent pig progeny-testing station in Denmark, and the first of its kind in the world, was built for use in 1907. By 1926, five such testing stations were in operation. In 1950, these five stations were replaced by three new identical stations constructed for individual feeding of all pigs under test.

The breeding centers are supervised by special committees and must submit groups of progeny (four littermates) of every approved boar and sow to one of the testing stations. The rate of gain and feed efficiency of each pig from a weight of 20 to 90 kg. live weight is recorded. The pigs are then slaughtered at cooperative bacon factories, where the carcasses

are examined the day after slaughter. This information is used as a basis of selecting breeding stock and to help breeders improve their herds.

Although the Danes attach great importance to fertility,²⁰ selection for milk-producing ability and fertility of sows has not been practiced less than selection for carcass quality. To enable a breeding animal to be approved or registered in the National Herd Book, however, certain minimum requirements for fertility and number of teats must be met. A committee visits the pig-breeding centers in its district twice each year to score and approve the animals approved for breeding. To be approved, the full pedigree for three generations must be known, with full information about each pig in the pedigree. The animal itself must be of good conformation (exterior), typical for the breed, and of good constitution. Each individual must have at least 12 teats, but at the present time most of them have 14, and some 16 to 18. Each dam in the pedigree must, as an average for all litters, have given birth to at least 10 and weaned eight pigs. In the pedigree, there must be testing results from the Progeny Testing Stations for the animals, and the records must not be inferior on important points to the average of all litters tested.

A summary of the preweaning performance of the Danish Landrace breed is given in Table 27. These data show a slow but steady increase in the number of pigs farrowed and weaned per litter from 1907 to 1951.

The improvement in pigs from breeding centers from 1926 to 1957 is given in Table 28.²¹ These data show that considerable improvement has been made for rate and economy of gain. A high degree of uniformity

FIGURE 54 EXCELLENT TYPE LANDRACE SOW WITH A GOOD UNDERLINE. (COURTESY AMERICAN LANDRACE ASSOCIATION.)



TABLE 27

PREWEANING PERFORMANCE OF THE DANISH LANDRACE BREED*

<i>Year</i>	<i>No. of litters</i>	<i>No. of pigs farrowed per litter</i>	<i>Pigs weaned at 8 weeks per litter</i>
1907	1,708	10.6	8.2
1927	2,815	10.9	8.4
1947	2,735	11.6	9.0
1951	3,673	11.7	9.4

*Reference 29.

has been obtained for body length, backfat thickness, and thickness of belly. The least improvement has been in body length and the most in backfat thickness.

The pig-breeding system practiced in Denmark has proved to be an effective method of carcass improvement, and the Landrace breed has changed considerably, although it still has not reached perfection. Many testing stations now located in the U.S. are patterned after those in Denmark, and should result in the production of a larger percentage of meat-type hogs. Most items concerned with type and conformation are highly heritable, indicating that progress should be made in selection for these traits. This is another reason why a conformation or type score should be included in a selection program, along with other items of economic importance.

TABLE 28

IMPROVEMENT IN DANISH LANDRACE PIGS
FROM 1926 TO 1956-57*

	<i>1926-27</i>	<i>1955-56</i>	<i>1956-57</i>
Daily gain, grams	623	680	684
Feeding units per kg. of live-weight gain	3.44	3.01	2.97
Length of body, cm.	88.90	94.10	94.20
Thickness of backfat, cm.	4.05	3.21	3.17
Thickness of belly, cm.	3.06	3.32	3.32
<i>Score from 0-15 for:</i>			
Shoulder	12.20	12.60	
Hams	12.30	12.60	
Fullness of meat	12.40	12.90	
Bacon type	12.20	12.70	
Percentage in grade A	50	92	

*Reference 21.

GENETIC CORRELATIONS AMONG TRAITS IN SWINE

Two methods may be used to estimate genetic correlations between traits. One of these is to use statistical procedures to estimate the probability that many of the same genes affect two traits. The other is to conduct experiments where selection is practiced for only one trait and then determine the correlated response of other traits as progress is made in selection.

Considerable evidence indicates that genes that promote rapid growth relative to body size cause more efficient utilization of the food consumed. This has been demonstrated by statistical studies¹¹ and by selection experiments. In the Illinois selection experiment¹ for rapid and for slow rate of gain, there was not only an average of 61.9 pounds difference in 180-day weights in the 8th to 9th generations, but the slow line pigs required 3.64 pounds of feed per pound of gain and the rapid line pigs required only 2.76 pounds of feed. In the Alabama selection experiment for efficiency of gains¹¹ pigs from the efficient line made daily gains of 1.40 pounds per day in the fifth generation of selection, while pigs from the inefficient line gained 1.24 pounds per day. In the Washington selection experiment for fast growth rate on a full feed and on a limited feed an increase in rate of gain through selection especially in pigs fed a limited ration, was accompanied by more efficient gains.

Some evidence for a negative genetic relationship between food utilization and maternal influence has been reported.^{11, 10} However, rate of gain and milk production seemed to be more nearly independent of each other genetically. A comparison of large type with small type swine indicated that the small type, which was thought to mature earlier, was poorer in milk production.²² This would suggest a possible negative relationship between early maturity and milk production.

A positive genetic correlation has also been reported between rate of gain and degree of fatness in pigs.¹¹ However, in an experiment in which selection was based only on backfat thickness as measured by probes in the live hog at a weight near 175 pounds² thinner backfat seemed to be correlated with thicker muscling, greater length of carcass and higher yields of lean cuts. In addition improvement in meat type seemed to be associated with faster rate of growth. Unpublished results from swine testing stations in the U.S. indicate rather clearly that meat type hogs grow as fast or even faster than lard type hogs.

INBREEDING RESULTS IN SWINE

Experiment stations in the Regional Swine Breeding Laboratory⁷ have been developing inbred lines and studying inbreeding effects. One hun-

dred twelve inbred lines were started at the various stations, some from purebred and some from crossbred foundations. In all cases, an attempt was made to obtain as good stock as possible from which to form the inbred lines. Many of the original lines were dropped after a year or two because of poor fertility or performance. Other lines were retained, and in some cases, two inbred lines were crossed to form a new inbred line. The results of these studies have shown that, although some inbred lines performed fairly well, there was a general decline in performance, with some traits being affected more than others. In addition, a few inherited defects due to recessive genes, such as hemophilia,⁷ were revealed and caused these lines to be discarded.

A summary of inbreeding effects on performance traits is given in Table 29. The data was obtained on 538 litters from four different stations, and the inbreeding ranged up to an average of 41.7 per cent for some of the lines. Inbreeding of the pigs affects their performance directly because of their genetic constitution, whereas the inbreeding of the dams affects the pigs through the maternal environment provided them from conception to weaning. It will be noted that the genetic constitution of the pigs, or their own inbreeding, caused a decrease in litter size at birth, 21, 56, and 154 days, with the effects becoming progressively less as the pigs grew older. This indicates that the vigor of the pigs was adversely affected by inbreeding, and the death loss before and after birth increased as the degree of inbreeding increased. The inbreeding of the pigs had little or no effect on their growth rate up to 56 days of age, but at 154 days there was 3.44 pounds less weight per pig for each 10 per cent increase in in-

TABLE 29

CHANGE IN PERFORMANCE FOR EACH 10 PER CENT INBREEDING FROM
INTRASEASON COMPARISON OF LINECROSSES
AND PARENTAL INBRED LINES*

	Inbreeding of.	
	Litters**	Dams***
Litter size at birth	-0.20	-0.17
Litter size at 21 days	-0.35	-0.31
Litter size at 56 days	-0.38	-0.25
Litter size at 154 days	-0.44	-0.28
Pig weight at birth (lbs.)	0.02	-0.06
Pig weight at 21 days (lbs.)	0.08	-0.11
Pig weight at 56 days (lbs.)	0.03	-0.06
Pig weight at 154 days (lbs.)	-3.44	-0.13

*Reference 12

**Litter size adjusted to zero difference in age of dam

***Dams adjusted to zero difference in litter inbreeding data

breeding. Inbreeding seemed to affect rate of gain less than it affected survival rate.

As shown in Table 29, inbreeding also affected the performance of the sow. Increased inbreeding of the sow resulted in a reduction in litter size and, to a lesser extent, the weights of the pigs. Since litter size up to the time of birth is determined by the ovulation rate and embryonic death losses, the results show that these factors were affected adversely by inbreeding. Maternal influences on pig weight after birth and up to 154 days of age are a reflection of milking and mothering ability of the sows. Inbred sows were inferior to non inbred sows in this respect.

Inbreeding also delays the onset of sexual maturity in gilts²⁷ and in boars.¹⁵ Reports from farms indicate that inbred boars do not perform as satisfactorily as non inbred boars because of a lack of mating desire, or libido. This causes a delay in the time of farrowing and may result in considerable economic loss, because pigs should be marketed at a definite time to command highest prices. For this reason, few inbred boars are sold for breeding purposes, and usually breeders prefer to sell line-cross boars. Inbred gilts generally produce fewer eggs during estrus and farrow smaller litters than those which are not inbred.

Inbreeding does not seem to have an adverse effect on economy of gains in swine.⁷ In fact, in some lines, economy of gain seemed to improve somewhat when inbreeding accompanied by selection for greater efficiency was practiced.

Few data are available on the influence of inbreeding on carcass quality, but this influence seems to be very small or nonexistent.

PERFORMANCE OF CROSSES OF INBRED LINES OF SWINE

The main purpose of developing inbred lines is to make the lines homozygous, these are then crossed to determine which combine well for commercial production. The actual performance of the inbred lines does not seem to be a good indication of their combining, or nicking, ability. Therefore, the only sure way to find if lines will "nick" is to cross them and observe the performance of the crossbred offspring.

Data summarized in Table 30 show the performance of inbred lines as pure lines and when combined in crosses. The inbreeding of each of the three lines ranged between 25 and 30 per cent. Their performance was poor as inbred lines, but when they were combined in a three-line cross using crossbred Landrace \times Poland sows as dams and Duroc boars as sires, performance was excellent. Thus, the performance of pigs depends not only upon the kind of genes they possess, but upon the ability of the genes to work together or complement each other when combined properly.

TABLE 30

ILLUSTRATION OF THE NICKING EFFECT OBSERVED FROM
CROSSING THREE INBRED LINES OF SWINE*

Characteristics	Inbred Durocs	Inbred Polands	Inbred Landrace	3-line cross	Avg. of 3-lines***	3-line cross as % of avg.
Number of litters	47	76	65	60		
Litter size at birth	7.59	7.61	8.67	9.94	7.87	126.3
Litter size at 56 days	5.26	4.57	6.15	8.39	5.31	158.0
Litter size at 154 days	4.77	4.16	5.45	8.06	4.79	168.2
Litter weight at birth (lbs.)	23.77	26.48	26.59	32.33	25.15	128.6
Litter weight at 56 days (lbs.)	170.78	168.03	224.32	326.12	183.48	177.7
Litter weight at 154 days (lbs.)	765.18	694.51	870.18	1544.58	773.76	199.6
Wt. per pig at birth (lbs.)	3.13	3.48	3.07	3.25	3.20	101.6
Wt. per pig at 56 days (lbs.)	32.47	36.77	36.47	38.87	34.55	112.5
Wt. per pig at 154 days (lbs.)	160.42	166.95	159.67	191.64	161.87	118.4

*Reference 22.

**Dams' records adjusted to a gilt basis but not adjusted for inbreeding of sow and litter.

***Calculated by giving one-half weight to Durocs and one-fourth weight each to Polands and Landrace. Thus, the calculated 3-line average has the same proportion of genes of each line as was present in the 3-line cross

Detailed studies of the performance of line crosses as compared to inbreds has been made at a number of experimental stations in the Regional Swine Breeding Laboratory.⁷ The results of these studies show that economic traits most adversely affected by inbreeding are those that show the greatest response when lines are crossed. Information on several of these experiments is presented in Table 31. Among the traits most responsive to crossing are litter size and weight at 56 days of age and post-weaning rate of gain. Efficiency of gains and carcass traits were improved very little by crossing.

However, line-cross pigs possessed more fat than inbred pigs. Similar results were also obtained²⁴ when Landrace \times Poland F_1 pigs were compared with the average of the inbred parent lines for backfat probes in live hogs at 200 pounds. In this study, crossbred pigs exceeded the average of the two parental lines by 6.5 per cent in backfat thickness measured only in inbred gilts of the two lines and gilts of the crosses of these two lines.

TABLE 31

VARIOUS TRAITS IN TWO-LINE CROSSES AS EXPRESSED AS A PERCENT-AGE OF THE AVERAGE OF THE TWO INBRED PARENTAL LINES*

Trait	<i>Two-line crosses as a per cent of the two parental inbred lines**</i>
Litter size at birth	108 5
Litter size at 56 days	120 8
Weight per pig at 56 days	112 3
Weight per litter at 56 days	139 8
Postweaning rate of gain	114 8
Postweaning efficiency of gain	105 4
<i>Carcass</i>	
Dressing percentage	100 9
Per cent lean cuts	100 0
Backfat thickness	104 7
Per cent fat cuts	101 6

*References 4 6 9 18 22 31

**Most data adjusted for age of dam where appropriate but not for inbreeding Part of the increase over the parental inbred lines therefore is heterosis and part is recovery from inbreeding effects

Sows from two-line crosses of the same breed have been bred to boars from a third line within that same breed and comparisons made between the performance of the two line and three-line cross pigs⁶ In this comparison at the Oklahoma Station the pigs of the three line cross had the benefit of having non inbred mothers The two-line cross sows definitely exceeded inbred sows in numbers of pigs farrowed and weaned They also exceeded non inbred sows of the same breed

Crosses of lines from different breeds usually show more hybrid vigor for litter size and growth rate than crosses within the same breed This suggests that for best results in crosses it is very important to cross those lines that are as far apart as possible in their genetic origin and relationship²⁶

Studies were made at the Purdue Station in which crosses of various inbred lines were compared with purebred non inbred controls and with crossbreds of the conventional purebreds These results showed that line-crosses of inbreds were superior to the controls especially in the number and weight of pigs raised to 154 days

TOPCROSSING

Topcrossing refers to the use of inbred boars on sows of various breeds which may or may not be inbred It is more practical to use inbred boars

for crossing purposes than it is to use inbred sows and gilts. The boar affects its offspring only in a genetic way, whereas the inbred sows and gilts must provide much of the environment for their pigs during both pregnancy and lactation. Since inbreeding causes a decline in vigor of the sows as well as of the pigs, inbred sows would be at a disadvantage from a practical standpoint as compared to non-inbred sows because of their inferior fertility and mothering ability. In addition, it would be more costly to furnish inbred sows to a farmer than it would inbred boars because of the larger number required and the greater expense of producing them.

The Wisconsin Station¹³ made a comparison of the progeny of inbred and non-inbred boars used in two-sire herds on Wisconsin farms. In this study, it was possible to compare records of test litters on the same farms in the same seasons. The data included records of 38 boars from several inbred lines and pigs from 680 litters produced on 44 farms. It was found that litters by inbred boars from four of the inbred lines definitely were superior to those of litters by non-inbred boars, as evidenced by the performance of their litters. It was concluded that inbred lines differ in their ability to combine with non-inbred stock. Thus, for topcrossing purposes, some lines are superior and others are not, and considerable testing is necessary to find those inbred lines with superior crossing ability.

In the same study¹³ 200 gilts from litters by inbred boars were compared with 238 litters by non-inbred boars on the same farms. Topcross gilts from inbred boars produced an average of one more pig per litter, and their litters weighed an average of 37 pounds more at weaning time.

CROSSBREEDING RESULTS WITH NON-INBRED STOCK

Many experiments have been conducted to determine the merits of crossbreeding for the production of market hogs. Much has been written about the pros and cons of crossbreeding. Commercial hog producers have used it as evidenced by the fact that approximately 85 per cent of the hogs in the United States marketed commercially are crossbreds.

Results of several studies of crossbreeding in swine are summarized in Table 32. In some of these studies, where only two-breed crosses were involved, both parental breeds were not available to compare with the performance of the F_1 . Since several studies were averaged, however, the performance of crossbred pigs as compared to purebred pigs from one of the breeds, especially that of the dam, should give a fair estimate of the amount of heterosis involved in a two-breed cross.

Heterosis from a two-breed cross represents increased vigor only in the crossbred pigs, since the dams in each case are purebreds. Results summarized in Table 32 show that litter size at farrowing was slightly smaller

TABLE 32

ILLUSTRATION OF THE AMOUNT OF HYBRID VIGOR* IN CROSSES OF NON-INBRED BREEDS OF SWINE**

<i>Traits</i>	<i>2-breed cross as a per cent of purebreds</i>	<i>3-breed cross as a per cent of 2-breed cross</i>	<i>3-breed cross as a per cent of purebreds</i>
Litter size at birth	99	108	107
Litter size at 56 days	119	123	142
Weight per pig at 56 days	107	100	107
Weight per litter at 56 days	128	123	151
Postweaning rate of gain	107	100	107
Postweaning efficiency of gains	99	101	100

*Hybrid vigor is estimated by subtracting 100 from each of the above figures.

**References 5, 17, 23, 25, 30.

in purebred sows bred to boars of another breed than in purebred sows bred to boars of the same breed. The difference is small and may be due only to sampling error.

Litter size at birth is determined by the number of eggs produced by the sow at the time of ovulation, by the number of eggs that are fertilized, and by the number of embryos and fetuses that survive to birth. In these experiments, since sows producing pigs were from the same breed, and within each experiment they were maintained under similar environmental conditions, ovulation rate should be the same regardless of whether sows produced crossbred or purebred pigs. If true, fertilization rate and the degree of embryonic death loss would be the two factors responsible for differences in litter size at birth between purebred and two-breed cross pigs. We can only conclude from the data presented that embryonic death loss seemed to be as great in crossbred as in purebred pigs. It should be pointed out, however, that a lower rate of fertilization when sows are mated to crossbred boars than when they are mated to boars of the same breed could reduce litter size at farrowing, even if embryonic death loss were greater in purebred pigs. We have no experimental evidence to offer that would suggest that this is true, however.

Litters of crossbred pigs from the two-breed cross averaged 28 per cent heavier at weaning than litters of purebred pigs. Most of this improvement was due to less mortality in the crossbred pigs between birth and weaning, but some of the improvement was due to their slightly heavier weaning weights. Crossbred pigs also made slightly faster gains from weaning to market weight, but there was little or no difference in the amount of feed required per unit of gain.

At the Iowa Station,²³ purebred sows were double mated, so that some of them produced both purebred and crossbred pigs in the same litters.

FIGURE 55 Two breed cross pigs out of a purebred sow only the offspring benefit in this case (COURTESY OF THE UNIVERSITY OF MISSOURI)



By making matings in this way, variations due to maternal environment could be controlled more accurately. The crossbred pigs from such matings were more vigorous at birth than purebred pigs in the same litters, and a larger percentage of those farrowed survived to weaning. Crossbred pigs also averaged about four pounds heavier than purebreds at weaning and made slightly faster and more efficient gains from weaning to market weight.

The performance of crossbred sows as compared to that of purebreds is shown in Table 32. This comparison is made by expressing the performance of the 3 breed cross as a percentage of that of the 2 breed cross. This gives an estimate of the advantage of crossbred over purebred sows.

Crossbred sows produced larger litters at farrowing than purebred sows, with the advantage averaging about eight per cent. The greatest advantage of the crossbred sows was in their ability to raise more pigs to weaning age. Crossbred sows exceeded purebred sows by 23 per cent in this



FIGURE 56 PIGS FROM A THREE BREED CROSS OUT OF A CROSSBRED SOW. THE THREE BREED CROSS GIVES ADDED HYBRID VIGOR IN THE SOW NOT FOUND IN THE TWO BREED CROSS (COURTESY OF THE UNIVERSITY OF MISSOURI)

particular trait. Most of the advantage of crossbred sows is evident by the time the pigs are weaned. Crossbred pigs from crossbred mothers gained no faster nor made more economical gains than crossbred pigs from purebred mothers.

A comparison of the performance of the three-breed crosses with that of purebreds gives an estimate of the combined hybrid vigor in both sows and pigs. This averaged 51 per cent for litter weight at weaning and is large enough to be of great value in commercial pork production.

CONCLUSIONS REGARDING CROSSBREEDING IN SWINE

The preceding discussion has shown rather clearly that the chief advantage of crossbreeding in swine production lies in the resulting increase in the size and weight of the litter at weaning and, in some instances, slightly faster rate of gain from weaning to market weight. Most of the advantage due to crossbreeding is due to the increased vigor of the pigs and, to a certain extent, the vigor of the crossbred sows.

Crossbreeding has certain disadvantages that should be pointed out. Quite often, crossbreeding results in the production of pigs that vary widely in coat color. Some people consider this a disadvantage, whereas others do not. It is possible, however, by watching the color of the breeds or lines used for crossbreeding, to control coat color so that it is uniform in the crossbred offspring. This may be done simply by using breeding animals all of one color or by using boars from a line or breed that is dominant in color to that of the sows used for breeding purposes. In the latter case, the boar must be homozygous dominant for all pigs to be of one color.

Crossbreeding alone will not cause much improvement in traits such as economy of gain and carcass quality. In other words, crossing parents from two families that are too fat will not give offspring of meat type. Or crossing two strains which are not efficient in their food utilization will not give efficient offspring. These traits must be present in the two strains or breeds that are crossed if they are desired in the crossbred offspring.

SYSTEMS OF CROSSBREEDING

To be successful, the commercial hog producer must follow a definite and systematic crossbreeding program. Several crossbreeding plans may be used for commercial pork production.

One plan is to use either purebred or very high grade sows and mate them to a purebred boar of another breed. This is referred to as a single

cross. The sire in this system of crossbreeding should come from breeds and herds which are superior in conformation and performance and especially noted for production of meat-type pigs. Sows should also be selected on a similar basis, but with special attention to fertility and nursing ability, along with performance and carcass quality. The chief disadvantage of this plan is that if it is followed in its entirety, all breeding stock must be discarded sooner or later, and the breeder must start over again. Another disadvantage of such a system of crossbreeding is that the swine producer does not take advantage of the hybrid vigor in the crossbred sows, because only purebred sows are used.

Another system of crossbreeding is referred to as "backcrossing" or "crisscrossing." In this system, a single cross between two breeds is made first, and from their offspring crossbred gilts are mated back to a boar of one or the other of the two original breeds. From the offspring of this mating, the crossbred sows are mated with a boar from the other of the two original breeds. This plan will result in about two-thirds of the inheritance of the pigs coming from the breed of the boar used last and one-third from the other breed. When this system is followed on a long-time basis, it should be possible to retain some of the hybrid vigor originally obtained in both sows and pigs, but some of this is lost after the first few generations.

A third and different system of crossbreeding is used quite widely by commercial swine producers. This is the three-breed or four-breed system of crossbreeding, in which purebred boars from the different breeds are used in rotation on selected crossbred sows. In this system of breeding, an attempt is made to retain the advantage from hybrid vigor that was attained when the first crossbred sows were used for breeding purposes. The optimum amount of hybrid vigor is attained with the three-breed cross, and after that in the four-breed or five-breed cross one merely attempts to retain that level in later generations. Contrary to the beliefs of some persons, using a three-breed or four-breed boar rotation as described above does not cause a decline in the level of heterosis after several generations if purebred boars are always used.

Regardless of the method of crossbreeding that is followed, it is extremely important to use as good breeding stock as possible, placing special emphasis on carcass quality and performance. Purebred boars should be used that are from strains of known superior quality and gilts should also be selected on this basis.

Breeds to use in rotation will depend a great deal on what is available to the commercial swine producer. In general, the principle to apply is to try each time to use a boar from a breed that is especially strong in points in which the previous boar or the gilts were the weakest. Not enough information is available to indicate for certain which breeds "nick" best in crosses. Actually, since breeds are not highly homozygous,

there may not be any breeds that "nick" better than others. Perhaps certain strains within each breed, however, do have better combining ability than others. If this fact is established, it should be exploited to the fullest extent.

KINDS OF GENE ACTION AFFECTING SWINE TRAITS

Having discussed the heritability of traits and inbreeding and crossbreeding effects on these traits in swine, we should be in a position to make some estimate of the kinds of gene action that affect the important economic traits in swine. Each trait may be affected by several kinds of gene action, but the proportional influence of some may be greater than others. Data are summarized in Table 33 to show these effects.

Litter size and weight at weaning seem to be affected greatly by non-additive gene action, which includes dominance, overdominance, and epistasis. The evidence for this is that the heritability of these traits is low and effects of inbreeding and crossbreeding have considerable influence on these traits. Little progress could be made in selection for these traits by mating the best to the best; the most improvement would come from crossing distinct lines from different breeds that genetically are as unlike as possible, to take advantage of heterosis. To improve these traits,

TABLE 33

KINDS OF GENE ACTION AFFECTING IMPORTANT ECONOMIC TRAITS IN SWINE

Trait	Heritability	Effects of:		Proportion of genetic variation due to different types of gene action	
		Inbreeding	Crossbreeding	Nonadditive	Additive
Litter size and weight at weaning	low	large	large	large	small
Rate of gain, weaning to market wt.	moderate	moderate	moderate	moderate	moderate
Economy of gain, weaning to market wt.	moderate to high	small	small	very small	large
Conformation	high	moderate	moderate	moderate	large
Carcass quality	very high	very small	very small	very small	large

crossing, and not selection within a pure line, strain or breed, should be practiced

Rate of gain from weaning to market weight is about 30 per cent heritable and is affected only moderately by inbreeding and crossbreeding. This suggests that both nonadditive and additive gene effects are moderate, and that some progress should be made by selecting for improved rate of gain through selection on the basis of individuality and families within a pure line. Some improvement could also be made in this trait by crossing lines of known superior combining ability.

Economy of gain from weaning to market weight is affected little by inbreeding and crossbreeding, and the heritability of this trait is about 38 per cent. Therefore, the evidence indicates that economy of gain is affected mostly by additive gene action, and selection for this trait within a pure line should be moderately effective. Possibly this trait would be more highly heritable if environmental variables such as feed wastage could be controlled more effectively. Results of the Danish Pig Testing Stations²⁹ indicate that considerable progress has been made in selecting for this trait, with feed requirements per pound of live weight gain being reduced from 3.44 to 2.97 in the past 30 years.

Heritability of carcass quality in swine seems to be high and inbreeding and crossbreeding effects very small. Thus, the additive type of gene action seems to be very important for this trait, and selection on the basis of family is the method indicated. Selection on individuality cannot be practiced, *because the trait cannot be measured until after death, with the exception of backfat, which can be measured in the live animal.* That selection for improved carcass quality is effective is borne out by the results in Denmark, where considerable progress has been made through selection on the basis of family.²⁹ The meat-hog certification program of the various breed associations in the United States is based on the high heritability of most carcass traits, and progress is being made in finding within the breeds those strains of inherent superior meat type, and the numbers of meat type hogs is being increased by this selection procedure.

Items associated with conformation are, in general, highly heritable, but little has been reported concerning inbreeding and crossbreeding effects. It would seem, however, that any decline in vigor, such as observed on inbreeding, would result in less desirable conformation. This is particularly true of sound feet and legs and bloom of the coat, which is associated with vigor. Crossbreeding, on the other hand, should improve some items of conformation *because of increased vigor, and might be more favorable to the development of sound feet and legs, especially if these traits are influenced by recessive genes.* The high heritability of most items of conformation, however, indicates that considerable progress should be made in selection for these traits within pure lines, strains, and breeds.

Since different kinds of gene action are of more importance for some economic traits than for others, and since each requires a different kind of selection and breeding method to make the most improvement, how can we make the best possible use of this knowledge in over-all swine improvement? This is an important question, because we do not select for one trait alone in swine, but are interested in several. The answer is that obviously we must apply as much selection pressure as possible in our pure breeds for those traits that are highly heritable and are affected by additive gene action. This should result in the improvement of such traits in our pure strains and breeds. Then, to take advantage of heterosis in traits such as litter size and weight at weaning, we must cross those lines that are superior in the other traits such as carcass quality, economy of gain, and, to a lesser extent, rate of gain. Obviously, if crossing has very little or no effect on these traits, we can expect the crossbreds only to equal the average of the parent lines or breeds for these particular traits. This is an important point often overlooked by breeders, for they do not understand that crossbreeding does not improve all traits.

Because some strains and breeds seem to be considerably superior to others in degree of fertility, more satisfactory results should be obtained when lines or breeds are crossed which are of high fertility. Heterosis effects, in addition to the average effects of the parents, should give much more satisfactory results for this trait than the crossing of two lines or strains that are decidedly inferior in fertility and prolificacy.

PROGRAMS FOR SWINE PRODUCTION

The foregoing discussion of breeding and selection systems for swine make it very obvious that improvements can be made in swine through attention to breeding methods, but improvement will be much slower in some traits than others, and different systems of breeding and selection may be required for each. The kind and amount of selection to apply will depend upon the purpose for which the animals are produced or the objective the breeder has in mind. Attention to disease control, management, and proper nutrition geared to the needs of the animals at various periods during life are necessary for a successful pork-production enterprise. We shall outline only those factors related to the improvement of swine through breeding methods.

PRODUCTION OF PUREBRED SWINE

The first step in swine production of any kind is to set up a system of record-keeping for each pig and sow in the herd. Examples of records are shown in Figure 57. At birth, each pig in the litter should be given an individual number, and the date recorded.

Records should be obtained on the daily rate of gain from shortly after weaning to a market weight of near 200 to 220 pounds. Efficiency of gain made during this period would also be desirable but seldom can be obtained for each individual pig because it is not practical to feed them individually. If this cannot be done, it would be desirable to feed pigs by litters and obtain the amount of feed required per 100 pounds of gain by the entire litter. Sometimes this is a problem because of the necessity of feeding boars and gilts together, which may result in some of the gilts being bred before the final weight is obtained. Boar and gilt pigs may be fed separately if the breeder desires, and if trouble is experienced with the boars ranting toward the end of the feeding period, final weights should be taken so records can be made before this occurs.

If room is not available to feed entire litters, samples of two to four pigs per litter from several litters by the same sire may be fed together. Although the economy of gain by litters will not be obtained by such a method, it may be obtained for different sire groups, where more than one sire is used for breeding purposes in a given season.

Several precautions should be taken to insure comparable records for litter or sire groups. Comparable beginning and ending weights for all pigs are necessary, and all pigs should be fed the same ration and handled in the same manner so as to hold environmental variations to a minimum.

FIGURE 58 THE AMOUNT OF BACKFAT IN THE LIVE ANIMAL MAY BE MEASURED BY USING A METAL PROBE OR RULER WHICH MEASURES TO THE NEAREST TENTH OF AN INCH (COURTESY OF THE UNIVERSITY OF MISSOURI)



Purebred pigs that are being tested should be fed and handled in as nearly as possible the same manner as their offspring will be.

Type scores should be obtained on all pigs at near 200 pounds and recorded for selection purposes.

Backfat probes on all pigs taken at three different sites when they weigh about 200 pounds are of considerable use for determining the degree of fatness in breeding groups or individuals. The probes at the three different sites may be averaged for each pig and the average figure used for comparative and selection purposes. Research data indicate that barrows will have from 0.25 to 0.35 inches more backfat than gilts and boars, and this should be given consideration when individuals or litters are compared. This suggests that a boar's barrow offspring will usually have from 0.25 to 0.35 inches more backfat than he possesses; for this reason, it is well to select for the thinnest backfat possible in boars if other traits are also desirable.

Records on carcass data are of considerable value in selection whenever they can be obtained under practical conditions. Carcass data on not less than two pigs per litter should be obtained. Slaughter weights should range from 200 to 220 pounds, and records on length of body, depth of backfat, and the area of the loin-eye muscle should be obtained. When possible to obtain them, the percentages of lean and fat cuts would be very desirable.

The information listed in the preceding paragraphs should be used to select those breeding animals with the superior performance and carcass quality. When new breeding stock is obtained, purchases should be made, when possible, from breeders who keep records as those listed in this section.

PRODUCTION OF MARKET HOGS

Since commercial pork production requires the greatest efficiency possible, some system of crossbreeding should be followed. But even if this is done, it is still extremely important to use superior stock for breeding purposes. Most breeders will find it desirable to retain females from their own herd for replacement purposes, because they have records on the herd and their relatives and the animals are better adapted to the conditions of the farm where they have been produced. Insofar as practical, the commercial producer should keep the same records as the purebred breeder.

The commercial pork producer relies almost entirely on the purebred breeder for the boars he uses in his herd. He is interested, therefore, in obtaining production-tested boars fed in the same manner as the pigs will be that he intends to produce for the market. Many commercial producers are purchasing top boars from the swine-evaluation stations now

operating in various parts of the country. Boars from certified meat-type litters should also be used whenever it is possible to obtain them.

A three-breed rotation system of crossing is now very popular in the United States. This system takes advantage of hybrid vigor in both sows and pigs, and although most of the advantage is gained in the first three crosses, proper emphasis on selection of boars and sows will almost maintain this advantage in later cycles of the rotation. Such a system naturally brings up the question of what breeds and lines should be used in the crossing program. At the present time not enough data are available on different breeds to make sound recommendations, but some general principles may be followed. Regardless of the breed, boars should be selected from strains where the sows are prolific and good mothers and where pigs make rapid and efficient gains and possess good carcass quality. Boars should be selected that are especially strong in those qualities in which the sows are weak. Obviously, the various breeds that have boars of this kind must be available in his area if the commercial pork producer plans to use them for crossing purposes.

Still another point to consider in the choice of breeds to use in a cross-breeding program is how far apart the breeds are genetically. In other words, were they developed in different countries from different genetic material? Research work shows that the greatest improvement from crossing is obtained from crosses of this kind.

Some of the new breeds of swine have been developed to be used for crossing purposes, and producers of seed stock of this kind can make recommendations to individual pork producers as to what breeds to use in a rotation system. The producer of seed stock is very careful about his recommendations, because later sales will depend upon whether or not his customers are satisfied.

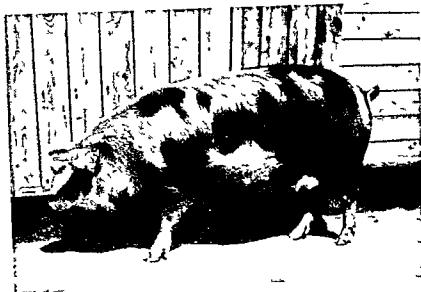


FIGURE 59 MINNESOTA No. 3 GILT FROM ONE OF THE NEWER SWINE BREEDS (COURTESY OF THE ANIMAL HUSBANDRY DEPARTMENT, UNIVERSITY OF MINNESOTA.)

good meat type. In addition, many of them were developed by means of performance-testing the breeding stock, and as a result, their production is at a desirable level.

In spite of the fact that the new breeds are inbred, most of them perform very satisfactorily from the standpoint of litter size at weaning and the rate of gain from weaning to market weight. As might be expected, however, there are differences between individual pigs within each breed. Information about the new breeds is given in Table 34. Many of

TABLE 34

NEW BREEDS OF SWINE IN THE UNITED STATES

<i>Breed</i>	<i>Foundation breeds and percentage contribution</i>	<i>Year breed began</i>	<i>Year breed recognized</i>	<i>Per cent inbreeding when recognized</i>
Minnesota No. 1	Tamworth 52% Landrace 48%	1936	1946	32
Minnesota No. 2	Canadian Yorkshire 40% Poland 60%	1942	1948	28
Montana No. 1	Hampshire 45% Landrace 55%	1936	1948	32
Maryland No. 1	Berkshire 37% Landrace 63%	1940	1951	30
Beltsville No. 1	Poland 25% Landrace 63%	1935	1951	35
Beltsville No. 2	Danish Yorkshire 58% Duroc 32% Landrace 5% Hampshire 5%	1940	1952	35
San Pierre	Berkshire 7% Chester White 7%	1950	1953	26
Palouse	Chester White 47% Landrace 53%	1945	1956	9

TABLE 35

PERFORMANCE OF SOWS FROM NEW BREEDS AS COMPARED TO THOSE FROM OLDER BREEDS*

Characteristics	Purebreds not inbred	New breeds or lines
Number of litters farrowed	4435	3180
Number of litters weaned	4203	2985
Number of pigs farrowed	36965	28463
Number of pigs weaned	25933	20418
Percentage of pigs weaned	70.2	71.7
Number of pigs farrowed per litter	8.33	8.95
Number of pigs weaned per litter	6.17	6.84
Percentage of litters weaned	94.80	93.90

*Data in this table adapted from reference 8 Table 2 page 275

the new breeds were developed specifically for crossbreeding purposes and some of them are used in rotation crossing systems at the present time. Some of the new breeds have become more popular than others because of the more desirable traits they possess and because of their crossing ability. A summary of the production of new breeds as compared to the old breeds in the United States is presented in Table 35.

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Questions and Problems

- 1 What is meant by economic traits in swine?
- 2 What does total litter weight at weaning tell us about the performance of swine?
- 3 Discuss some of the difficulties encountered in measuring the efficiency of gains in swine
- 4 What is gained by feeding pigs individually as compared to feeding them in a group?
- 5 Would selection for improved rate of gain cause a corresponding increase in the efficiency of gain? Why?
- 6 List those important economic traits that possibly can be improved by selection in a purebred herd. Why can they be improved?
- 7 What important economic traits are improved by crossbreeding? Why?
- 8 How do we know whether or not improvement in swine performance in Danish Swine is due to heredity or environment or both?
- 9 What are the main effects of inbreeding in swine?
- 10 What is meant by topcrossing and how may it be used to advantage in swine production?

11. Outline the different systems of crossbreeding in swine. Which of these would you recommend to the commercial pork producer and why?
12. Outline in detail a breeding system for the production of purebred swine.
13. Outline in detail a breeding system for commercial swine production.
14. Why is it important to know something about the kinds of gene action affecting important economic traits in swine?

23

Systems of Breeding and Selection in Beef Cattle

INFORMATION ON BEFF CATTLE BREED-

ing is not as complete as that on swine. One reason for this is that extensive and cooperative efforts toward a comprehensive study of breeding principles in beef cattle were initiated relatively recently. Another reason is that progress is slower in beef cattle breeding because the interval between generations is considerably longer in cattle than in swine, and cattle are much less fertile than swine. Cattle usually produce only one calf per year, whereas a sow may produce two litters per year, each consisting of eight to ten pigs.

Much work is now being done in beef-cattle breeding, and considerable progress has been made in developing breeding principles for this species. In this chapter, important beef-cattle breeding principles will be presented, and it will be shown how they may be used for improving the performance and carcass quality of this species.



FIGURE 60 THESE YEARLING STEERS HAVE BEEN GATHERED FROM THE RANGE AND ARE HEADED FOR THE SALES PENS MANY MILES AWAY. MUCH OF THE WESTERN RANGE COUNTRY PRODUCES SPLENDID FEEDER CATTLE FOR THE FATTENING PENS (COURTESY OF THE SAN CARLOS APACHE INDIAN TRIBE, SAN CARLOS, ARIZONA.)

prise. Because of the wide variety of conditions under which cattle are produced, methods of management and feeding may vary considerably from one locality to another. However, methods of breeding for the improvement of beef cattle are very similar in all areas.

The improvement of beef cattle through breeding methods requires that accurate and careful records be kept on all animals in the herd. This is done on many farms and ranches at the present time, and special attention is being paid to a few traits of the greatest economic importance. These traits will be discussed in the next few paragraphs.

FERTILITY

Fertility may be defined in numerous ways, but the definition used here is the percentage of calves raised to weaning age from all mature cows in the herd. Such a definition, of course, includes numerous factors, such as the ability of a cow to rear a calf to weaning and her ability to conceive while raising that particular calf. Of course, fertility in a herd is also dependent on management and nutrition factors and the ability of a calf to survive from birth to weaning.

Fertility as thus defined is one of the most important economic traits in beef cattle in all areas of the United States. In some areas, there is room for much improvement in this particular trait. A survey of the American National Cattlemen's Association in 1956⁸ showed that only 79 per cent of beef cows actually bred dropped live calves and only 62 per cent reared calves to weaning age.

The percentage calf crop is an important factor in the efficiency of production, because dry cows eat almost as much as cows nursing calves,



FIGURE 61 'EYE APPRAISAL' FOR PERFORMANCE IS OFTEN MISLEADING THE COW ON THE TOP WEANED A HEAVY CALF EACH YEAR FOR EIGHT YEARS THE COW ON THE SIDE WEANED ONLY FOUR AVERAGE WEIGHT CALVES IN THE SAME PERIOD OF TIME. RECORDS TELL THE STORY

and they yield nothing but their added weight for that particular year. If we assume that the cost of keeping a cow for a year is \$100, the cost of each calf weaned is strongly dependent on the percentage calf crop weaned as shown below ²⁸

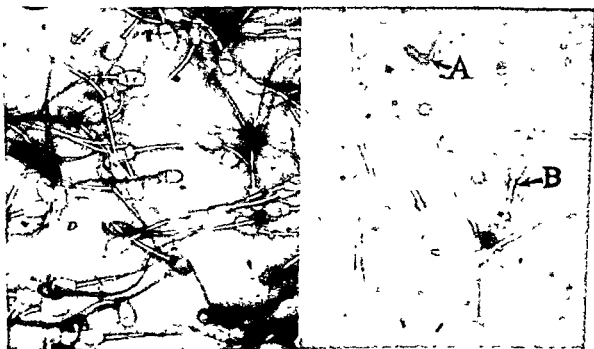
Percentage of calf crop weaned	Cost per calf weaned
100	\$100
90	\$111
80	\$125
70	\$143

beef cattle.³⁰ Such conditions are more or less self-limiting, because the homozygous recessive individuals are usually of low fertility (some are sterile) and leave fewer offspring in the herd.

The following points should be given consideration if the percentage calf crop is low and improvement is desired.

1. Thoroughly investigate the management of cows and bulls, making certain that enough bulls are turned in the breeding pasture each year to assure that every cow has a chance to be bred. When only one bull is used, observe cows as often as possible to make certain that they are not failing to conceive, as evidenced by their coming into heat at regular intervals during the breeding season. A fertility test on the bulls before the beginning of the breeding season will identify many of those of low fertility or those that are sterile.
2. Make certain that the nutrition level, quantity and quality, is adequate and that diseases which may affect fertility are not present in the herd.
3. Cull cows that are hard to settle or those that are dry two years in succession. This will remove all cows that are poor breeders because of disease, accidents (which may occur at calving time), and heredity. A pregnancy test each fall on all cows will identify those that are not pregnant; these can be marketed when fat without being fed another year.
4. Select breeding stock, both bulls and heifers, from cows that have a record of producing a good calf every year.

FIGURE 62 RIGHT, ABNORMAL SPERM OF THE BULL. (A), SPERM WITH A COILED TAIL AND (B), SPERM WITH A PROTOPLASMIC DROPLET NEAR THE BASE OF THE HEAD. LEFT, NORMAL SPERM OF THE RAM. THE STAINED CELLS WERE DEAD AND THE NONSTAINED CELLS WERE ALIVE WHEN THE SLIDES WERE MADE. (COURTESY OF THE UNIVERSITY OF MISSOURI.)



WEIGHT OF CALVES AT WEANING

The percentage calf crop and the weight of each calf at weaning, combined, are probably the two most important factors in beef-cattle production. The weaning weight of the calf is of importance, because this represents the pounds of production per cow per year. This trait depends on the milk production of the cow and, to a lesser extent, on the ability of the calf to make fast and efficient gains.

Data presented in Table 36 show that the heritability of differences in weaning weights in beef calves is about 25 per cent with a range in 11 different studies from -6 to +64. Thus this trait is affected to a certain extent by additive gene action but to a larger extent by environmental factors. Careful selection for this trait should result in some improvement over a period of years.

An average of seven different studies shows that weaning weights are about 46 per cent repeatable (Table 37). This means that the weaning weight of the first calf from a cow is a fairly good indication of the weaning weight of her later calves. Culling heifers or cows that wean light calves will tend to improve the over all average of the herd in later years with other factors remaining equal. The fact that repeatability estimates average much higher than the heritability estimates (almost twice in fact) indicates that the maternal influence of the cow is an important source of variations in weaning weights of calves. This influence is both environmental and genetic. The environmental aspect includes the nutrition of the embryo in the uterus and the influence on the calf after birth mostly through the milk production of the cow.

TABLE 36

HERITABILITY ESTIMATES IN PER CENT FOR VARIOUS ECONOMIC TRAITS IN BEEF CATTLE*

Trait	No of studies	Range	Avg
Weaning weight	11	- 6 to 64	25
Weaning score	8	23 to 53	33
Rate of gain in feed lot	10	26 to 99	57
Efficiency of gain in feed lot	5	17 to 75	36
Slaughter grade	4	38 to 63	47
<i>Carcass items</i>			
Dressing per cent	4	1 to 73	46
Carcass grade	5	16 to 84	48
Thickness of fat	1		38
Area of eye muscle	3		70
Tenderness of lean	2		61

*Averages from many reports

TABLE 37

REPEATABILITY ESTIMATES FOR ECONOMIC TRAITS IN BEEF CATTLE*

<i>Trait</i>	<i>No. of studies</i>	<i>Range</i>	<i>Average</i>
Calving interval	2	- 9 to 2	4
Interval from exposure to bull and calving	4	14 to 38	28
Weaning weights	7	40 to 52	46
Weaning scores	2	19 to 21	20

*Average of data from several sources.

In selecting breeding stock for heavy weaning weights, all calves must be compared on as nearly the same basis as possible, and those with superior weaning weights retained for breeding purposes. In making comparisons, corrections should be made for as many important factors as possible. One important phase of research in beef-cattle breeding has been to identify factors of importance in causing variations in weaning weights and to develop methods of correcting for them so that comparisons of individuals within a herd are more valid.

All calves should be weighed as near the same age as possible. Some breeders prefer a standard age of 180 days, whereas others prefer 210 days. Determining the weight of each calf on a particular day of age would require that calves be weighed each day from the time the first one born reached the standard age previously decided on until the youngest one reached this age. Correction factors have been developed so that the members of an entire herd can be weighed all on one or two days, and the individual weaning weight corrected to a standard age basis. The following formula may be used for correcting calves' weights to a 210-day basis:

$$\text{Corrected 210-day weight} = \frac{\text{Weaning Wt.} - \text{Birth Wt.}}{\text{Age in days}} \times 210 + \text{Birth Wt.}$$

To correct to a 180-day basis, one merely needs to replace the 210 with 180.

Weaning weights of calves should also be corrected for sex before selections are made. Correction factors for this purpose have been developed by the South Dakota Experiment Station⁷ and are as follows:

Adjust to a bull basis (for purebred herds where bulls are kept) by

1. Adding 45 pounds to heifer weights, or

2. Adding 30 pounds to steer weights.

Adjust to a steer basis in herds not keeping bull calves by adding 15 pounds to heifer weights.

The age of the dam is an important source of variations in weaning weights of calves and corrections should be made for this before records of individual calves and cows are compared. The South Dakota Experiment Station has also published correction factors for this purpose⁷ and these are as follows

Age of dam in years	Amount to add to weaning weight (pounds)
2	60
3	40
4	20
5-8	0
9	10
10	25
11	35
12	50

Adjustment for sex, age of calf and age of dam are the only ones recommended at the present time and corrections for these will make comparisons for weaning weights more indicative of the producing ability of the cows and the genetic worth of the calf.

The following points are suggested to improve the weaning weights of calves through attention to breeding methods

- 1 Identify each cow and her calf by a tattoo, brand or some other means
- 2 Keep continuous accurate records on each calf and correct weaning weights for age of dam, sex of calf and age of calf
- 3 Keep replacement heifers insofar as possible from those calves with the heavier weaning weights
- 4 Cull cows especially younger ones that produce a light calf at weaning
- 5 Select herd bulls of superior type and performance from a herd where complete and accurate records are available and from cows which have demonstrated their ability to produce a heavy calf at weaning year after year

RATE AND EFFICIENCY OF GAIN IN THE FEED LOT

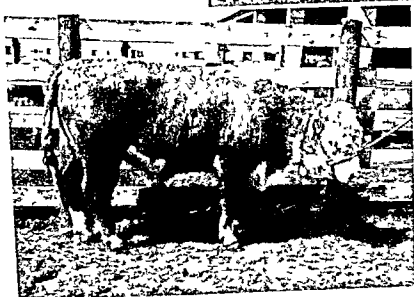
The ability to make fast and efficient gains in the feed lot is an important trait in beef-cattle production. This has been recognized for many years by beef cattle feeders. It has also been noted that there is considerable variation among different steers in their ability to make fast and efficient gains when placed on a full feed in the feed lot.

Many cattlemen have contended that it is possible to select the faster gaining and more efficient animals by paying attention to conformation. Many studies, however, show rather clearly that this is not the case and that selection for performance on the basis of conformation is ineffective.

Experimental research work at the U.S. Range Livestock Experiment Station, Miles City, Montana, several years ago indicated that the ability



FIGURE 63 BOTH OF THESE BULLS WERE FED THE SAME RATION IN THE SAME BARN FOR THE SAME LENGTH OF TIME. THE BULL AT THE TOP, HOWEVER, GAINED 3.22 POUNDS PER DAY AS COMPARED TO 1.79 FOR THE BULL AT THE BOTTOM. MUCH OF THIS DIFFERENCE WAS PROBABLY DUE TO INHERITANCE. (COURTESY OF THE UNIVERSITY OF MISSOURI)



to make fast and efficient gains in the feed lot was more prevalent in the progeny of some bulls than in the progeny of others.¹³ A later study of data from the same station,²⁹ in which results were presented for eight steers each from 13 different sires fed during 1948 and 1949, showed striking differences among progeny of different sires. When the progeny of the best bulls and those of the poorest were compared, there was a difference of 211 pounds in the final feed-lot weight, 0.43 pounds per day in average daily gains, and \$45 in the returns per head above feed costs. Thus, for eight steers, one bull sired progeny which yielded \$360 more above feed costs than those of another bull.

Many later studies indicate that the ability to make fast and efficient gains in the feed lot is highly heritable (Table 36). Therefore, bull calves that make fast gains should sire calves that make fast gains under the same conditions. This has led to the feeding of bull calves under standard periods and conditions; this practice is known as performance-testing. Heifers usually are not full-fed on test because of the time and expense involved and because it is possible that a highly fitted condition might interfere with their breeding efficiency. Cattlemen in some areas try to obtain performance-tested bulls and pay a premium for those with superior records. It should be mentioned here, however, that performance-

testing of bulls does not make them any better genetically. It merely gives a bull a chance to show whether or not he possesses the inherent ability to make rapid and efficient gains. Before purchasing a performance tested bull, one should make sure that he has a good record.

A strong correlation exists between the ability to make rapid gains and the ability to make efficient gains in the feed lot. A summary of six studies³⁴ showed an average correlation coefficient of 0.45 and a range from 0.06 in one study to 0.69 in another. This degree of correlation suggests that bulls selected for rapid gains are likely to make efficient gains, although the correlation is not perfect. If further research work indicates that the correlation is high enough, individual feeding may not be required so that bulls can be fed in groups and only the rate of gain during a certain period measured. This would be much simpler and considerably less expensive than individual feeding.

One important question is whether animals of superior inherent gaining ability can be identified as accurately by feeding them a limited ration as by feeding them all they will eat. In one study,⁴¹ the heritability of gain on a limited ration in dry lot was 34 per cent, and in the same steers later on a limited ration on pasture, the heritability of gains was 43 per cent. Many of the same genes seemed to be responsible for fast gains during both periods. In another study,¹⁸ it was found that animals making the fastest gains on the range also tended to make the fastest gains in the feed lot.

The heritability estimates for gains made on a limited ration on dry lot or on pasture were high enough to indicate that considerable progress could be made by selecting the faster-gaining cattle on such feeding regimes. These heritability estimates, however, are considerably lower than estimates for cattle on a full feed. Although more data are needed to answer this question, it seems that the most progress would be made by full feeding cattle for a minimum of 150 days and then selecting those which made the fastest gains. Since such a practice is often impractical on the farm, the next best plan would be to select the animals that made fast gains on either pasture or a limited ration.

On the basis of evidence at hand, the following recommendations should be made on the performance testing of animals:

- 1 Feed only bulls that show promise from the standpoint of their own individuality and that of each parent.
- 2 Bulls to be compared should not vary in age by more than one or two months.
- 3 Bulls to be compared should have a similar pretest environment. That is, do not compare bulls which have been creep-fed with those which have not. Other things being equal, thinner calves should make faster gains on feed.
- 4 Use average of two weights taken at least two days apart for the initial

- and for the final test weights Bulls should be shrunk on weigh day for 6 to 12 hours Differences in fill can account for as much as 40 to 60 pounds of apparent gain
- 5 Use the same feed for all bulls and see that they have equal opportunity to get their share of feed This is usually done by feeding in individual stalls two or more times per day Many prefer to feed a complete mixed ration of chopped hay and grain rather than to feed hay and grain, free-choice This controls the ratio of hay to concentrate, for, if fed free-choice, some animals would eat more roughage than others and would make less rapid gains Some prefer to feed a pelleted ration,²⁷ which has resulted in very rapid gains with very little feed wastage
 - 6 Animals should be fed for at least 150 days, and at the end of the test the daily rate of gain and the feed required per 100 pounds of gain should be calculated A final type score should also be taken These three measurements can be used in an index to select the top bulls for breeding purposes
 - 7 Most heifers are not full fed as are bulls, but it is possible and of considerable value to obtain gain tests on them by measuring gains made on pasture during the spring and summer months

TYPE

By type is meant the body form and structure supposed to be ideal for the purpose for which the animal is produced It includes something more than just size and scale, type is estimated by visual appraisal and cannot be measured by a ruler or tape

Type has been used very widely in the past for the selection of breeding stock Perhaps the main reasons for this are that a visual appraisal is rather simple to make and that the price per pound of feeder and slaughter animals is dependent to a considerable extent on this particular trait In spite of the popularity of type, however, it has been shown time and time again to be inadequate as a criterion for selecting animals that are best suited for the feed lot and for the packer and retailer A more adequate and accurate measurement of performance in the feed lot is to record the rate and efficiency of gain as discussed previously Carcass quality can best be measured after the animal is slaughtered This phase of beef-cattle production will be discussed in a later section

Various experiment stations have used type scores and slaughter grade scores based on visual appraisal in research studies in the past several years One of the methods of scoring used is presented in Table 38 Experimental data³⁴ indicate that type-score and grades are subject to considerable error, in that the agreement among different judges for the same animal is difficult to achieve, and the repeatability of the score of the same judges on the same animal at different times is low Undoubtedly, the condition of the animal at the time of scoring is a factor, for fat imports a pretty color, and even an excellent animal appears mediocre when it is thin and in poor condition

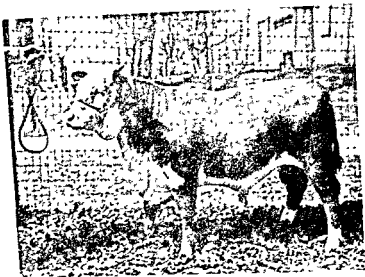
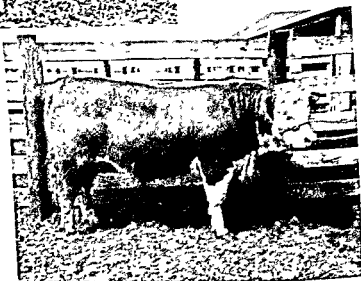


FIGURE 64 THESE BULLS GAINED AT THE SAME RATE ON AN INDIVIDUAL FEEDING TEST, BUT THE ONE AT THE TOP HAD A MUCH HIGHER CONFORMATION SCORE. IF BOTH TYPE AND FAST GAINS ARE DESIRED, THEY MUST BOTH BE SELECTED FOR SINCE THEY SEEM TO BE INHERITED INDEPENDENTLY. (COURTESY OF THE UNIVERSITY OF MISSOURI.)



Type-scores are often taken at weaning time and, for bulls, at the end of the feeding period when they have been on test. Many experiment-station workers have given steers a score for slaughter grade that is often similar to scores given to bulls at the end of the feeding trials.

Data summarized in Table 36 show that weaning score is about 33 per cent heritable, whereas slaughter grade is about 47 per cent heritable. Both are highly enough heritable so that they should be improved through selection. Since type is of considerable economic importance, it is well to use this trait in the improvement of beef cattle through breeding. Scores at weaning and at the end of the feeding period should be taken on as many of the animals in the herd as possible.

The tendency of beef-cattle producers recently toward marketing cattle at a younger and lighter age has resulted in the production of cattle that mature earlier and are blockier in type and conformation than those of several years ago. As a result, breeders have emphasized selection for width, depth, and compactness in their breeding animals. The controversy as to which is most desirable, the small, blocky type, the large, rangy type, or the intermediate type, led to research work in which animals

TABLE 38
BEEF-CATTLE SCORING FORM

Fancy +	15
Fancy	14
Fancy -	13
Choice +	12
Choice	11
Choice -	10
Good +	9
Good	8
Good -	7
Medium +	6
Medium	5
Medium -	4
Common +	3
Common	2
Common -	1

of the various types were compared. The American Hereford Association⁴² sponsored a test at the Kansas, Oklahoma, and Ohio Experiment Stations to determine what type or size of animals should be the most desirable from the standpoint of rate and economy of gain and finishing ability. In this study, it was found that steers sired by large bulls made faster gains than those sired by medium-size and small bulls. Likewise, steers sired by medium-size bulls gained faster than steers sired by small bulls. These gain advantages were more pronounced during the wintering and grazing phases of the growth period than during the full-feeding phase. Over-all differences among the three groups in the economy of gains were not significant, but when the ration consisted of a large portion of roughage or grass, the small bulls produced progeny that made more costly gains. The results indicated that the medium-size cattle were the most desirable, because they tended to combine the gaining ability of large cattle and the finishing ability of small cattle without a lowered efficiency of gain.

Another study,⁵ at the Oklahoma Station, compared conventional-type Herefords with comprest-type. The mating of comprest bulls to comprest cows resulted in a lower reproductive performance and a lower calving percentage, apparently due to one or more forms of hereditary dwarfism. Calves produced by the comprest matings that were not dwarfs either were comprests or resembled calves from conventional Herefords. These large-type calves were definitely superior to their comprest half-sibs in rate and economy of gains in the feed lot, but the comprests attained a finish at an earlier age. Similar results were obtained when comprests were compared with calves from the conventional-type line.

A similar study at the Colorado Station³⁹ showed that the small, compact types weighed about 20 per cent less at weaning and slaughter than conventional type cattle, but they had about the same feed efficiency and the same percentage of higher-priced cuts. More calving difficulties in the compact cows and the occurrence of dwarfism made them less profitable than conventional cattle.

A study at the New Mexico Station,¹⁷ in which the performance of large- and small-type cattle was studied over a period of several years, showed that the large cows were superior to the smaller, more compact cows in the percentage calf crop weaned and in longevity.

Past experience indicates that selecting for the small, compact, quick-maturing type of cattle may lead to an increase in the frequency of occurrence of some kind of dwarfism. For this reason, perhaps the intermediate type of beef animal would be the most desirable in the long run.

CARCASS DESIRABILITY

The final criterion in judging beef cattle is quality of the meat they produce at slaughter. The previous discussion has dealt with the efficiency of production; the discussion now will deal with the end product, the actual meat produced.

At the present time, breeding animals cannot be selected on the basis of carcass quality, because this can be determined only after death. No good method has yet been developed for the determination of carcass quality in the live animal, even though studies have been directed toward this objective and valuable methods may be obtained in the future. For this reason, then, selection of breeding animals for carcass quality must be based on progeny or sib tests.

Methods of evaluating carcass quality in steers to meet consumer pref-

FIGURE 65 LOIN EYE AREA AS DETERMINED IN THE LIVE ANIMAL BY MEANS OF THE SONORAY (UNBROKEN LINES) AS COMPARED TO THE ACTUAL LOIN EYE AREA MEASURED IN THE CARCASS AFTER SLAUGHTER (BROKEN LINES) THE TOTAL AREA VARIED ONLY 0.1 OF AN INCH (COURTESY OF THE ANIMAL HUSBANDRY DEPARTMENT, UNIVERSITY OF MISSOURI.)

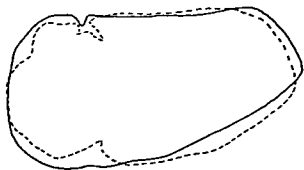
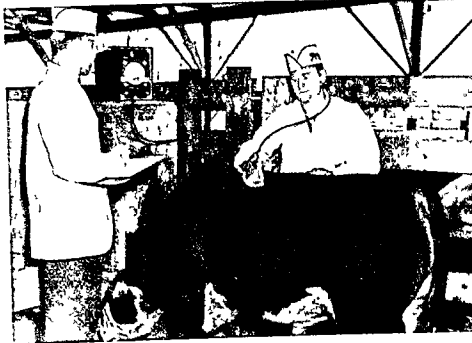


FIGURE 66 MEASURING THE LOIN EYE AREA IN THE LIVE ANIMAL BY MEANS OF THE SONORAY. (COURTESY OF THE UNIVERSITY OF MISSOURI.)



erence for different kinds of meats are now receiving attention. In addition, emphasis is being placed on the determination of conformation characteristics in the live animal that are related to a higher percentage of the high-priced cuts of meat.

Heritability estimates for certain items of carcass quality are given in Table 36. Most of these estimates are high enough to indicate that progress could be made in selecting for these traits and that much of the variation is due to the additive effect of genes.

FREEDOM FROM INHERITED DEFECTS

Another important economic trait in beef cattle is the freedom from certain inherited defects that interfere with performance and fertility. Most of these are probably inherited as recessive traits and will be of no great significance unless the heterozygote is preferred in selection.

That detrimental recessive genes are probably carried by many breeding animals has been shown to be true when progeny tests have been made by mating sires back to their daughters. Progeny-test records on six bulls selected at random showed ²⁵ that each was carrying from one to four recessive genes with undesirable effects. Recessive genes, however, need not cause too much concern, because inbreeding is seldom practiced in commercial beef production. Outbreeding reduces the chances that the recessive alleles will be combined, thus inhibiting the phenotypic expression of these genes.

The most important inherited defect in beef cattle known to date is snorter dwarfism. It has caused an enormous loss to the beef-cattle industry and has concerned almost every beef-cattle breeder either directly or indirectly. Much research to determine the physiological cause of dwarfism has been done and is still being done. The use of pedigrees and progeny tests in selecting breeding stock have helped to limit it, but even so the

incidence is still of considerable importance. Evidence seems to indicate strongly that heterozygotes are preferred in selection.

Defects apparently of a recessive nature have been reported for beef cattle in various parts of the world. Many of these affect fertility and have been of importance in some countries.

A defect inherited as a dominant trait should cause little concern to a breeder, because such a trait is expressed by the phenotype and the genes for it may be discarded from the herd merely by culling all animals which show the trait. This kind of inheritance is more complicated, however, when penetrance is not complete and when the genes vary in their expression. Here, the phenotype may not indicate the presence of the genes, and yet the genes for the trait will be transmitted to the offspring.

The use of artificial insemination has heightened the concern over increasing the frequency of detrimental recessive genes in the population. One male may be used to sire several thousand calves in his lifetime. If he is heterozygous for a particular trait, according to the laws of chance, one-half of his offspring will receive the recessive gene from him. The author knew of one case in which a bull, later proven to be heterozygous for the snorter dwarf gene, produced 600 calves in one season without siring a single dwarf. When his sons and daughters were mated to other heterozygotes, or when a certain amount of inbreeding was practiced, many dwarfs were produced. Thus, hundreds of carriers of a recessive gene were introduced into a herd in one year's time.

FIGURE 67 Two half sisters that have had a long and productive life in the same herd. Longevity should be given attention in selection, especially if it is accompanied by high production.



LONGEVITY

This is another trait of considerable importance to the beef-cattle breeder. Beef animals that have a long and productive life should be used as sources of replacement stock whenever possible, even though they themselves may not appear to be outstanding from the standpoint of conformation. These animals show that they possess the inheritance for longevity, and they probably do not carry detrimental genes of partial dominance or detrimental genes that express themselves only later in life. They also show that they may possess the genes for good performance.

The opportunity for selection for longevity in beef cattle is greater than in most other classes of livestock. There is especially little opportunity to select for this trait in hogs, for a boar and sow are usually discarded after they have produced a few litters, because of their extreme size. In addition, the boar is often sold because he has so many daughters in the herd he can no longer be used without practicing inbreeding.

CORRELATION AMONG PERFORMANCE TRAITS IN BEEF CATTLE

Animal breeders are becoming more and more aware of the fact that genes that control the expression of one quantitative trait are quite likely to influence the expression of others. This may be due to the close biochemical and physiological relationships among various life processes. The realization of this has led to the measurement of genotypic, phenotypic, and environmental correlations among traits.¹⁰ Some research on these factors has been done in beef cattle.

PHENOTYPIC CORRELATIONS BETWEEN TRAITS

Phenotypic correlations between traits are the gross correlations that include both the environmental and the genetic portions of the covariances. Phenotypic correlations for traits are important because they directly affect the size of the selection differentials when several factors are used in a selection index. This is especially true when the correlation is high, whether it is positive or negative.

A summary of many studies in which phenotypic correlations between various traits have been reported is given in Table 39. Of particular interest in these correlations is the positive relationship between rate of gain and efficiency of gain and between slaughter grade and some of the other items of carcass quality. A higher slaughter grade is associated with a higher carcass grade, a higher dressing percentage, slightly greater rib-eye, and more fat on the outside of the carcass. This would indicate that

TABLE 39

PHENOTYPIC CORRELATIONS BETWEEN ECONOMIC TRAITS IN BEEF CATTLE

	Wean wt.	Wean score	Rate of gain	Efficiency of gain	Slaughter grade	Carcass grade	Dressing per cent	Area of rib eye	Thickness of fat
Wean weight	1 00	0 26	0 16	- 0 40	- 0 05	0 43	-	0 32	0 26
Wean score		1 00	- 0 05	- 0 04	0 28	0 20	-	-	-
Rate of gain in feed lot			1 00	0 51	0 09	0 32	- 0 14	0 36	- 0 07
Efficiency of gain in feed lot				1 00	0 15	0 02	- 0 24	0 07	- 0 03
Slaughter grade					1 00	0 64	0 38	0 29	0 50
Carcass grade						1 00	0 45	0 07	0 54
Dressing per cent							1 00	0 36	0 25
Area of rib eye								1 00	0 01
Thickness of fat									1 00

Most of the correlations represent averages from several studies many of which were summarized in references 6, 33, and 35

slaughter grade is one of the better indicators of carcass desirability in the live animal, and attention to this correlation, until a better measure is found, will be of great importance in selecting meat animals.

GENETIC CORRELATIONS AMONG TRAITS

By genetic correlations is meant the probability that the same gene, or genes, affects two or more traits.

Many of the same genes which affect growth during pregnancy also seem to affect growth rate from birth to weaning.^{20,22} After weaning and during the feed-lot period, many of the same genes affect growth rate. In one study, steers were fed after weaning for 252 days and the period divided into three 84-day periods. The genetic correlations between the various periods ranged from 0.45 to 0.82,¹⁴ indicating that many of the same genes affected the growth rate in the three different periods. Similar conclusions were made in two other studies.^{32,41} Genetic correlations between preweaning and postweaning gains and type scores were large in another study.²⁰ This seems reasonable, because one would expect the fast-gaining calves to show more desirable beef characteristics than unthrifty, slow-gaining calves.

In beef cattle, there is some evidence that there may be a genetic antagonism between high milk production and fast growth rate.²¹ Such an antagonism would mean that an improvement through selection for greater milk production in cows would result in a simultaneous decrease in the rate of gain by the calves produced by these cows. However, more research needs to be done to clarify and prove this point.

EFFECT OF INBREEDING ON PERFORMANCE TRAITS IN BEEF CATTLE

As compared to swine, very little is known about the influence of inbreeding on the most important economic traits in beef cattle. In three studies,^{4,19,26} a decrease in weaning weight varying from 4.8 to 17.5 pounds for each 10 per cent increase in inbreeding of the calf was observed. On the other hand, a 10 per cent increase in the inbreeding of the dams resulted in a decrease of 11.5 pounds in the weaning weights of their calves in one study,⁴ whereas an increase of 9.50 pounds was found in another.²⁶ Inbreeding had no effect on type-score in the latter study.

No figures for effects of inbreeding are available on the other performance traits in beef cattle. The genetic history of the Line 1 Hereford cattle at the U.S. Range Livestock Experiment Station at Miles City, Montana, gives some information on this point.¹⁵ This report includes in-

formation on the line from 1936 to 1949. During that time, the inbreeding increased slowly and gradually until, in 1948, the average of the herd was 15.95 per cent. Record of performance results indicated that the line increased in rate of gain in the feed lot and in weight for age without much apparent loss of quality of carcass. (Selection had been made for weight for age and rate of gain mostly in the sires, with little selection pressure on the females.) Progress actually made was as great as or even greater than expected as calculated from heritability estimates, selection differentials and generation intervals.) Apparently, selection for performance was effective in spite of an increase in inbreeding, and may suggest that inbreeding did not have an important effect on weight for age or rate of gain in the feed lot in this line.

At the Colorado Station³⁹ the weight of calf weaned per 100 cows was almost 43 per cent greater from crosses of inbred sires on unrelated line-cross cows than it was from inbreds. Most of this advantage was due to a 30 per cent greater calf crop and 10 per cent heavier weights. The line-cross calves also outgained and scored higher than the inbreds. These data suggest some effect of inbreeding on these particular traits.

CROSSBREEDING IN BEEF CATTLE

Most of the crossbreeding work in beef cattle has been done in the South and Southwest, where Brahmans have been crossed with native and British breeds of cattle. Only a few experiments have been done where British breeds have been crossed among themselves and data obtained from the crossbred cows and calves.

Very few crossbreeding experiments have been reported where crossbred calves and purebred calves from the two parent breeds have been produced concurrently. Such data must be available to get an estimate of heterosis. Most reports compare only purebred calves of one breed with crossbreds. An average of several studies of this kind should give a fairly valid estimate of heterosis and, from a practical standpoint, indicate the merit of crossbreeding as compared to inbreeding.

FERTILITY

No data could be found in the literature in which the percentage calf crop from purebred and crossbred parents could be compared. In the Ohio Experiment¹¹ however, 94.9 per cent of the crossbred calves from the purebred Hereford and Angus dams survived to weaning as compared to an average of 91.7 per cent of purebred calves from the two breeds. This study was conducted over a period of eight years and 205 purebred and 196 crossbred calves were produced during the course of the experiment.

WEIGHT OF CALVES AT WEANING

Data from several sources summarized in Table 40 shows the advantage of crossbred calves at weaning over purebred calves from the same breed of dam. In all instances, the crossbred calves averaged heavier than the purebred calves. Crossbred calves of the British breeds averaged 4.3 per cent heavier than purebreds, whereas those of crosses of British cows with non-British bulls averaged 15.5 per cent heavier. Thus, a greater advantage was noted in the use of non-British bulls, although it is not known if the same results would have been obtained if the experiments had been run in the Midwest where conditions are more favorable to the British breeds than are the hotter regions of the U.S.

Only in the Ohio Experiments¹¹ were data available in which the average of the crossbred calves could be compared with the average of the purebred calves from the two parental breeds to get an estimate of heterosis. In this experiment, heterosis in weight of calves at weaning was calculated from their data and found to be 3.61 per cent.

Experiments are summarized in Table 41 to show the performance of crossbred cows as compared to purebred cows with purebred calves. In none of these experiments was it possible to get an estimate of heterosis, because data on only one purebred parental breed were available. Nevertheless, crossbred cows had a definite advantage over purebred cows, with an average advantage of 22.2 per cent in the weight of their calves at weaning. Thus, much of the increase in weaning weight when crossbreeding is practiced seems to come from the use of crossbred cows which

TABLE 40
INFLUENCE OF THE CROSSBREEDING OF THE CALF
ON WEANING WEIGHTS

Breed		Crossbreds as per cent of purebreds*	No of studies	References
Sire	Dam			
Brahman	Angus	116	1	1
Africander	Angus	115	2	1, 28
Zebu	Angus	123	1	28
Hereford	Angus	102	1	11
Brahman	Hereford	108	2	30, 24
Angus	Hereford	106	1	11
Shorthorn	Hereford	105	1	16
Average of British crosses		104.3		
Average of British × non-British		115.5		
Average for all		110.7		

* Purebreds were the same breed as the dam in all cases

TABLE 41

INFLUENCE OF THE CROSSBREEDING IN COWS ON THE WEANING WEIGHTS OF THEIR CALVES

Sire	Dam	Crossbreds as per cent of purebreds*	References
Angus	Brahman × Angus	134	1
Hereford	Brahman × Hereford	124	30
Hereford	Brahman × Hereford	120	24
Angus	Shorthorn × Hereford	113	16
Hereford	Angus × Hereford × Shorthorn	120	16
Average of British crosses		116.5	
Average of British × non-British crosses		126.0	
Average of all		122.2	

* Comparisons were made with purebred cows and calves so this includes heterosis in both cows and calves

are either better milkers or better mothers. This could be of great importance in commercial beef production.

RATE OF GAIN IN THE FEED LOT

Crossbred calves seem to have some advantage over purebreds in the feed lot, although this advantage is not large and not always consistent. Data summarized from several experiments where purebred calves were compared with crossbred calves in the feed lot are given in Table 42. Again, this is a comparison with only one parental breed and cannot be taken as an actual measurement of heterosis. In these experiments crossbreds gained, on the average, 6.2 per cent faster than did purebred calves.

Estimates of heterosis are given in Table 42 where the crossbred calves could be compared with the average of the parental breeds in the feed lot. The average value was -1.5 per cent, although in four experiments three showed a slight amount of heterosis. These limited data suggest that there is very little heterosis for rate of gain in the feed lot for beef cattle.

EFFICIENCY OF GAINS IN THE FEED LOT

Crossbreeding does not diminish the amount of feed required to make 100 pounds of gain, as shown in Table 43 and Table 44. In fact, crossbreds seem to require a little more feed than purebreds. If this is the actual case it might be explained by the fact that crossbred calves weigh

more at weaning than purebred calves and are therefore in better condition at the beginning of the feeding period. It is well known that the amount of feed per unit gain increases as animals increase in weight and become fatter. Presumably, fatter animals require more feed per pound of gain, because approximately 2.25 times more energy is required to lay down a pound of fat than a pound of muscle. This difference in feed requirements is not great enough, however, to be a great handicap to the crossbred animals, since they have other advantages which offset this slight disadvantage.

CARCASS QUALITY

The only controlled experiment in which carcass data for animals from the two parental breeds was compared with the carcass data of crossbreds was reported by the Ohio Station¹¹ for Hereford, Angus, and the reciprocal crosses between these two breeds. Detailed carcass data were not re-

TABLE 42

INFLUENCE OF CROSSBREEDING ON RATE OF GAIN IN THE FEED LOT

Comparisons of Crossbreds with Only One Purebred Parent Breed:

Purebred	Crossbred	Crossbreds as per cent of purebreds	References
Hereford	Shorthorn × Hereford	96	12
Hereford	Shorthorn × Hereford	97	12
Hereford	Shorthorn × Hereford	110	16
Hereford	Angus × (Sh. × Her.)	108	16
Hereford	Her. × (Ang. × Sh. × Her.)	111	16
Hereford	Hereford × Brahman	87	12
Hereford	Hereford × Brahman	102	12
Angus	Brahman × Angus	107	1
Angus	Africander × Angus	105	1
Average		102.6	

*Comparisons of Crossbreds with Average of Purebred Parent Breeds:**

Crossbreds	Crossbreds as per cent of purebreds	References
Hereford × Brahman	101	12
Angus × Hereford	102	11
Angus × Holstein	89	9
Angus × Arkansas Natives	103	37

*The comparison of the purebred parents with the reciprocal crosses gives an estimate of heterosis

TABLE 43

INFLUENCE OF CROSSBREEDING ON THE POUNDS OF FEED REQUIRED
TO MAKE 100 POUNDS OF GAIN IN THE FEED LOT

<i>Comparisons of Crossbreds with Only One Purebred Parent Breed:</i>			
<i>Purebred</i>	<i>Crossbred</i>	<i>Crossbred as per cent of purebred</i>	<i>References</i>
Hereford	Shorthorn × Hereford	103	12
Hereford	Shorthorn × Hereford	99	12
Hereford	Shorthorn × Hereford	101	16
Hereford	Angus × (Sh. × Her.)	105	16
Hereford	Her. × (Ang. × Her. × Sh.)	103	16
Hereford	Hereford × Brahman	113	12
Hereford	Hereford × Brahman	99	12
Angus	Brahman × Angus	101	1
Angus	Africander × Angus	105	1
Average		103	

<i>Comparison of Crossbreds with Average of Purebred Parent Breeds*</i>		
<i>Crossbred</i>	<i>Crossbreds as per cent of purebreds</i>	<i>References</i>
Brahman × Hereford	106	12
Angus × Hereford	100	11

*Gives an estimate of per cent heterosis. Note that it is negative.

ported, but the crossbreds averaged 60.55 per cent in dressing percentage, as compared to 60.00 for the purebreds, for an advantage of about 0.5 per cent. Approximately 74 per cent of the crossbreds were in the choice grade at the end of the feeding trials, as compared to 69 per cent of the animals from the pure breeds.

Experiments in which crossbreds were compared with one parental breed are more numerous. In U.S.D.A. experiments,¹⁶ the crossbreds averaged a little higher than the purebred Herefords in carcass grade at the end of the feeding period. The dressing percentage also averaged a little higher in the crossbreds (Table 45).

A summary was made of data from a number of agricultural experiment stations in which carcass quality was compared in pure British and British × Brahman crosses at weaning and after fattening in the feed lot.⁴⁰ At weaning, the crosses exceeded the British breeds in dressing percentage, percentage of preferred cuts, percentage of hind quarter, percentage of lean cuts, and area of the rib eye. They contained less fat cuts and less bone than the British breeds. At slaughter, after being fed in the

TABLE 44

AVERAGE OF CROSSBREDS AS COMPARED TO THE AVERAGE OF THE TWO PUREBRED PARENTS IN THE OHIO CROSSBREEDING EXPERIMENTS*

Trail	No. of calves		Avg. of purebreds	Avg. of crossbreds	Crossbreds as per cent of purebreds
	Purebred	Crossbred			
Gestation	201	196	281.35	282.66	100.47
Birth weight	205	196	64.00	64.60	100.94
Weaning weight	188	186	421.45	436.65	103.61
Per cent born survived weaning	205	196	91.71	94.90	103.48
Daily gains birth to weaning	188	186	1.58	1.66	105.06
Daily gains on pasture	85	92	1.02	1.03	100.98
Daily gains in feed lot	187	186	1.64	1.68	102.44
Feed/100 lbs. gain	187	186	1098.00	1094.00	99.64
Dressing per cent	180	185	60.00	60.55	100.92
Per cent graded choice	180	185	69.44	73.97	106.52

*Reference 11.

feed lot, the Brahman crosses exceeded the British steers in dressing percentage, percentage of preferred cuts, percentage of hind quarter, percentage of fat cuts, and area of rib eye. The crosses had about the same percentage of lean cuts but about one per cent less bone than the British steers. Carcass grades and live animal scores at weaning and at slaughter were about the same for the British and the Brahman crosses

TABLE 45

CROSSES AS A PER CENT OF HEREFORDS*

Trail	First cross Short. × Hereford	Second generation Ang × Sh × Her	Third generation Her × Ang × Sh
Birth weight.	106.0	96.9	100.9
Weaning weight	105.0	112.7	120.3
Final feed lot weight	107.8	109.9	113.9
Daily feed lot gain	110.2	107.5	110.9
Gain per 100 lbs. Total	100.8	95.1	96.7
Digestible Nutrients	102.0	103.4	102.3
Dressing per cent.			

*Reference 16

TABLE 43

INFLUENCE OF CROSSBREEDING ON THE POUNDS OF FEED REQUIRED
TO MAKE 100 POUNDS OF GAIN IN THE FEED LOT

<i>Comparisons of Crossbreds with Only One Purebred Parent Breed:</i>			
<i>Purebred</i>	<i>Crossbred</i>	<i>Crossbred as per cent of purebred</i>	<i>References</i>
Hereford	Shorthorn × Hereford	103	12
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Hereford	Shorthorn × Hereford	101	16
Hereford	Angus × (Sh. × Her.)	105	16
Hereford	Her. × (Ang. × Her. × Sh.)	103	16
Hereford	Hereford × Brahman	113	12
Hereford	Hereford × Brahman	99	12
Angus	Brahman × Angus	101	1
Angus	Africander × Angus	105	1
Average		103	

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<i>Crossbred</i>	<i>Crossbreds as per cent of purebreds</i>	<i>References</i>
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Angus × Hereford	100	11

*Gives an estimate of per cent heterosis. Note that it is negative

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*Reference 11.

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CONCLUSIONS ON CROSSBREEDING IN BEEF CATTLE

Although there is much more to be learned about the various aspects of crossbreeding in beef cattle some facts are fairly clear. Evidently, cross breeding produces the highest weaning weight in calves. It may also increase fertility. Crossbred calves generally show much more vigor than purebreds up to the time of weaning especially when Brahmans are involved in the crosses. This could be because the Brahmans can transmit their ability to resist heat and other adverse environmental conditions prevalent in the South and Southwest where these studies have been made.

Crossbred cows also seem to be better mothers than purebred cows from comparisons made to date but more work is needed before we can state for certain just how superior the crossbred mothers are to the purebreds.

Crossbreds seem to be slightly superior to purebreds in postweaning rate of gain and in carcass grade but possibly require more feed per 100 pounds of gain. These advantages and disadvantages seem to counterbalance each other for the important postweaning characteristics. The fact that advantages for the crossbreds come early and mostly before the calves are weaned may cause some persons not to recognize this advantage when all the emphasis is placed upon feed lot gains. Heavier weights at weaning result in heavier weights at the end of the feeding period even if the daily gains during this period are no faster than in purebreds. If crossbreds do not sell for less per pound at weaning because they are crossbreds this system of production seems to offer definite advantages for more efficient beef production.

The very high heritability estimates for rate of gain in the feed lot and for most carcass traits together with medium to high estimates for efficiency of gains indicates that for the present at least considerable improvement in these traits can be made within the pure breeds. Therefore selection of breeding stock should be made with this goal in mind. The improvement of purebreds would still be very desirable even if cross breeding becomes the breeding system of choice in the future. The most efficient production results even when crossbreeding is practiced when both parents are superior for the important economic traits.

KINDS OF GENE ACTION AFFECTING ECONOMIC TRAITS IN BEEF CATTLE

The kinds of gene action of importance in the phenotypic expression of the various economic traits in beef cattle are summarized in Table 46. Although much more information on beef-cattle breeding is needed at

TABLE 46

KINDS OF GENE ACTION THAT SEEM TO BE THE MOST IMPORTANT IN
THEIR EFFECT ON CERTAIN ECONOMIC TRAITS IN BEEF CATTLE

Trait	Degree of Heritability	Effects of		Proportion of genetic variation due to different types of gene action	
		Inbreeding	Crossbreeding	Nonadditive	Additive
Weight of calves at weaning	medium	large	large	large	medium
Weaning score	medium	low	unknown	unknown	medium
Rate of gain in the feed lot	high	probably low	small	small	very large
Efficiency of gains in the feed lot	medium to high	small	small	small	large
Slaughter Grade	high	unknown	unknown	small	large
Carcass items	high	probably small	probably small	small	large

F , the number of days to bring each animal to a low choice slaughter grade and E , the amount of feed per pound of gain. To illustrate the calculation of such an index, let us assume the following

$$\begin{aligned} W &= 400 \text{ lbs} \\ R &= 2.5 \text{ lbs} \\ F &= 200 \text{ days} \\ E &= 7.5 \text{ lbs} \end{aligned}$$

The calculated index would be

$$\begin{aligned} I &= 0.58(400) + 18.64(2.5) - 0.73(200) - 5.87(7.5) \\ &= 232 \quad + 46.6 \quad - 146 \quad - 44.03 \\ &= 88.57 \end{aligned}$$

This index is given only as an example, to show how several important factors can be considered in the construction of an index so as to aid in selection for maximum genetic progress. It may or may not be applicable to the selection of beef cattle in areas other than the region for which it was constructed or for traits other than those selected for here.

SUGGESTED PROGRAM FOR PUREBRED BEEF CATTLE PRODUCTION

The extension divisions of most states in the U.S. have outlined beef cattle improvement programs for their respective states. Therefore a complete program in every detail will not be given here. Some important points to consider in a beef improvement program will be given, however, along with sample record forms in Figures 68 and 69.

- 1 Identify all animals with a tattoo brand or some other means
- 2 Record the exact birth date of each calf, tattoo at birth and record the numbers of both the calf and the cow
- 3 Obtain a weaning score and weight and correct the weights of calves for age of dam, age of calf and sex of calf
- 4 Retain replacement heifers from those with the heaviest weaning weights and best type-scores
- 5 Cull cows after one or two calf crops that consistently wean calves lighter than the average of the herd. The amount of culling will depend upon available replacement stock and upon whether the herd is increasing in numbers or is remaining stationary in size. (Cull on the basis of records and not on type alone)
- 6 Weigh and score heifers again at approximately 18 months of age to obtain information on their rate of gain after weaning and on records of sire groups as well as information on gaining ability of calves from different cows. Cull those heifers with undesirable type or gains or with obvious undesirable traits

Date _____

Year _____ Breed _____

Year _____ Breed _____

Name _____ Address _____ Year _____ Breed _____

Name _____ Address _____ Year _____ Breed _____

[illegible]

FIGURE 68 SAMPLE RECORD FORMS FOR RECORDING DATA ON CALVES FROM BIRTH TO WEANING.

FIGURE 69 SAMPLE FORMS FOR RECORDING POSTWEANING PERFORMANCE IN BEEF CATTLE.

7. Feed all bull calves that are superior from the standpoint of type and weaning weight. If they cannot be fed individually, feed them as a group, but give all bulls an equal chance at the feed bunk. Feed for at least 150 days, and at the end of the feeding period, calculate the rate and efficiency of gain, and score for type and conformation. Rank the bulls in order for the traits of most economic importance and keep the best for breeding purposes
8. In purchasing herd bulls, obtain them from a herd where records of the kind mentioned above are kept. Obtain the best bull possible on the basis of type, and rate and efficiency of gain at the end of a feeding test. Select a herd bull from a cow that has a lifetime record of producing a calf each year that is superior in type and weaning weight.

NEW BREEDS OF BEEF CATTLE

Some new breeds of beef cattle have been developed recently in the South and Southwestern parts of the United States using the Brahman in crosses with other breeds, mostly those of British origin. The Brahmans can withstand the adverse conditions in that part of the country and transmit this ability to their offspring.

SANTA GERTRUDIS

This breed was developed by the King Ranch of Kingsville, Texas, from a cross between Shorthorn cows and Brahman bulls.³¹ Its development involved an exploratory phase in which crosses of Brahmans and British breeds were made. This was followed by the multiplication of the progeny of individuals shown to be superior on the basis of progeny tests, accompanied by inbreeding, linebreeding, and selection.

FIGURE 70 EXCELLENT TYPE BRAHMAN COW. (COURTESY OF THE KOONTZ RANCH, INEZ, TEXAS.)





FIGURE 71 PUREBRED SANTA GERTRUDIS COW, AGE 38 MONTHS AND WEIGHING 1590 POUNDS (COURTESY SANTA GERTRUDIS BREEDERS INTERNATIONAL, KINGSVILLE TEXAS)

In 1940 30 years after the first exploratory matings of a Brahman bull with purebred Shorthorn cows, the Santa Gertrudis breed was recognized as a new beef breed. Santa Gertrudis are red in color and are considered to be $3/8$ Brahman and $5/8$ Shorthorn. The breed is very well adapted to the region where it was developed as well as to other regions of a similar environment. Mature steers and cows average approximately 200 pounds heavier than animals of the British Breeds of the same sex and age.

CHAROLAIS

This is a French breed that was developed in the latter part of the 18th century. It was originally used for draft purposes as well as for beef production. The Charolais varies from white to a light straw color and reaches a very large size at maturity.

FIGURE 72 PUREBRED CHAROLAIS COW TWO YEARS AND NINE MONTHS OF AGE WEIGHT 1734 POUNDS (COURTESY OF THE LITTON CHAROLAIS RANCH CHILLICOTHE MISSOURI)



The breed in the United States has been developed from a few individuals imported before laws were passed restricting the importation of breeding stock from countries where foot-and-mouth disease was prevalent. The Charolais breed in the United States may carry genes from other breeds because of the small number of imported purebreds available to breeders in this country. The American International Charolais Breeders Association registers purebred animals and those that are produced by a topcrossing program and possess from 1/2 to 31/32 Charolais genetic inheritance. Certificates for animals produced by topcrossing must give the exact percentage of Charolais inheritance as well as that of the other breeds involved. An animal which possesses 31/32 Charolais inheritance is considered to be a purebred.

BRANGUS

The Brangus originated from a cross of the Brahman and the Angus. They are black and naturally polled and retain many of the characteristics of the original parent breeds. The International Brangus Breeders Association has its headquarters in Kansas City, Missouri. Registered Brangus are those bred as a breed for several generations or those produced by starting with purebred Angus and purebred Brahman if regulations of the association are adhered to. Figure 74 shows how Brangus may be produced by two different methods by combining the two parent breeds.

CHARBRAY

This is an American breed developed by combining the Charolais and Brahman breeds. The American Charbray Breeders Association will reg-

FIGURE 73 EXCELLENT TYPE BRANGUS BULL. (COURTESY OF THE BRUCE CHURCH RANCH, INC., YUMA, ARIZONA.)



ister animals that have from $3/4$ to $7/8$ Charolais inheritance, with $13/16$ Charolais and $3/16$ Brahman being the proportion of inheritance that seems most desirable. The breed is horned and is white to light straw in color.

BEEFMASTERS

This new breed was developed from crosses among Brahmans, Short horns, and Herefords. The development of the breed was begun in 1908 by E. C. Lasater of Falfurrias, Texas, and has been continued since 1930.

FIGURE 74 MATING SYSTEMS FOR THE PRODUCTION OF BRANGUS (COURTESY OF *The Cattleman*, FORT WORTH, TEXAS)

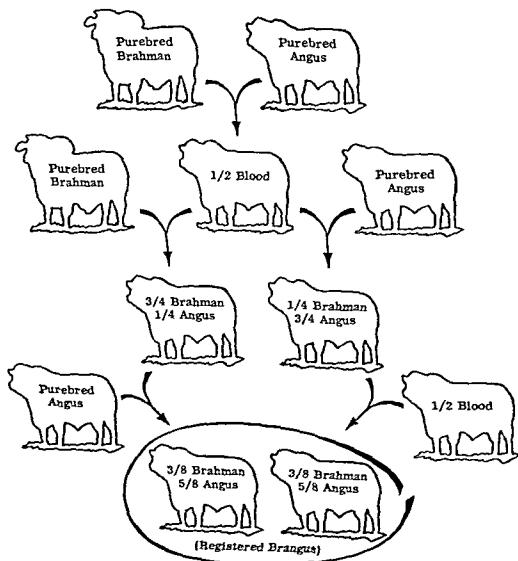


FIGURE 75 THE CHARBRAY IS A NEW BREED RESULTING FROM THE CROSSING OF THE AMERICAN CHAROLAIS ON THE BRAHMAN. THESE ARE EXCELLENT TYPE CHARBRAYS (COURTESY OF THE AMERICAN CHARBRAY BREEDERS ASSOCIATION.)



under the direction of his son. No attempt has been made to incorporate a definite percentage of inheritance from the three original breeds, although the genetic composition is probably approximately 50 per cent Brahman, 25 per cent Hereford, and 25 per cent Shorthorn.

Rigid selection for performance has been practiced within this breed, with special attention to disposition, fertility, weight for age, conformation, hardiness, and milk production. Much less attention has been paid to color and other fine points. Most Beefmasters are horned but some are polled, and some breeders are selecting for this trait. Although Beefmasters are recognized as a breed, no formal registry association has been formed.

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Questions and Problems

1. List the traits of greatest economic importance in beef cattle production.
2. Since the heritability estimates for fertility in beef cattle are low, what can be done to improve this trait?
3. What kind of gene action probably affects fertility in beef cattle to the greatest extent?
4. Outline adjustments necessary before weaning weight can be used as a criterion for selection.
5. Outline in detail a method of selection for the improvement of rate of gain of beef cattle in the feed lot.
6. What traits in beef cattle seem to be affected the most by inbreeding? By crossbreeding?
7. Outline in detail a breeding program for purebred beef-cattle production.
8. Outline in detail a breeding program for commercial beef-cattle production where steers are sold as feeders.

Systems of Breeding and ✓ Selection in Sheep

SHEEP WERE AMONG THE FIRST ANIMALS domesticated and have been raised by man for food and clothing for many centuries. Many references are made to the sheep industry in the Holy Bible many hundreds of years before the birth of Christ. The very nature and habits of sheep were so well known in the time of Christ that he used them as examples in his parables and other teachings.

Sheep were brought to the American continent by the early settlers. In fact, it is said that Columbus brought sheep with him on his second voyage to the new world in 1493. The number of sheep reached a peak of 56 million in 1942 in the United States. Since then, the number has declined to less than 30 million. The number is still large enough to make sheep one of the major sources of income from livestock in some areas.

TRAITS OF ECONOMIC IMPORTANCE

Sheep are produced for both mutton and wool. In general, mutton is not as popular as pork and beef, although it is the preferred meat in some countries. Wool for use in the manufacture of clothing and other textiles is being replaced somewhat by various synthetic fibers, but there is still a good demand for it in many parts of the world.

Traits of economic importance in sheep are those related to the cost of production of the kind of wool and mutton demanded by the consumer. These traits will be discussed separately as was done in the chapters dealing with other species of farm animals.

FERTILITY

Sheep are seasonal breeders and in most areas of the United States the breeding season is in the fall. Some breeds such as the Merino and Dorset Horn may be bred under some conditions to produce two lamb crops per year. Most breeds produce just one crop per year although rams produce sperm throughout the year. Some rams are susceptible to high summer temperatures however and may be infertile or of low fertility in late summer during the first part of the breeding season.

The number of lambs raised per ewe is one of the most important factors determining the efficiency of production. Lamb production varies a great deal under different conditions and with different breeds. Ewes under farm conditions are usually more prolific than those produced on the range. This is probably due to a higher level of nutrition generally found in farm flocks. Twinning in sheep often is desirable because a ewe that weans twins produces from 30 to 10 pounds more lamb than the ewe that weans a single lamb.

Extensive studies of breeding and lambing records have been made at the U. S. Sheep Experiment Station at Dubois, Idaho.¹⁶ Complete sterility of rams was rare and low fertility was uncommon. The percentage of ewes bred that lambled varied between 85 and 88 per cent for the different breeds. The percentage of lambs born per ewe lambing varied from 118 to 129. An average of 95 lambs was born per 100 ewes bred. Another study of records at the same station⁹ covering a 11 year period showed that 90.43 per cent of the ewes bred lambled with 92.54 per cent of the lambs born being alive at birth. The average percentage lamb crop

FIGURE 76 EWES OF EXCELLENT TYPE WITH TWIN LAMBS
A LARGE LAMB CROP WEANED SHOULD BE THE GOAL OF ALL
SHEEP BREEDERS (COURTESY OF THE UNIVERSITY OF MISSOURI)



weaned of the live lambs born was 82.52. In contrast to these figures, in a Missouri study, 1.61 lambs were born per ewe with 1.16 weaned.⁶

Fertility in sheep is lowly heritable, with an average heritability and repeatability estimate of 7 to 13 per cent. These estimates are in agreement with those for other classes of livestock. This indicates that fertility in sheep is not greatly affected by additive gene action and could be improved very little by selection. Most of the phenotypic variation, therefore, is due to environmental factors and attention to these should improve the lamb crop.

WEANING WEIGHT

The age at which lambs are weaned varies under different conditions, but the age of 120 days is often used for selection purposes.

Lambs can be weighed as they reach 120 days, or weaning weights can be corrected to this age. The correction is done by multiplying the average daily gain from birth to weaning age by 120 and adding this product to the birth weight. Weights of twins may be adjusted to a single-lamb basis by multiplying the adjusted 120-day weight by the factor 1.0529; for triplets the factor is 1.0923.

The age of the ewe may have considerable influence on the weaning weight of her lambs. Two-year-old ewes wean lambs that are from five to ten pounds lighter than those from mature ewes. Production of ewes usually increases to four or five years of age. Probably the most important adjustment is that for weaning weights of lambs from ewes that are two years of age. This adjustment can be made by comparing the production of the two-year old ewes with that of mature ewes in the same herd and then adding the difference to the weaning weights of lambs from the younger ewes. Or, if this is not possible, an adjustment may be made by adding seven pounds to the weight of the lambs.

Weaning weight in sheep is about 43 per cent repeatable (Table 47), which indicates that culling ewes from the herd on the basis of their first year's production is practical. Culling the poorly producing ewes will increase the average weaning weight of the entire herd thereafter if environmental conditions remain unchanged. Weaning weight in sheep is about 33 per cent heritable. Thus, selection for this trait will result in some improvement, although it may be slower than for postweaning gains or some other traits.

POSTWEANING GAINS

Some work has been done in performance-testing of sheep after weaning as has been done with beef cattle. Rate of gain in the feed lot in sheep is highly heritable, as shown in Table 48, so mass selection to improve

TABLE 47

ESTIMATES OF THE PER CENT OF REPEATABILITY OF ECONOMIC TRAITS IN SHEEP

Trait	No of reports	Average	Range
<i>Fertility</i>			
Lambing per cent	2	7	0 to 15
No lambs born	6	13	5 to 24
Birth weight	2	32	27 to 36
Weaning weight	5	43	22 to 76
Yearling body weight	3	73	71 to 78
Body type	2	33	26 to 40
Condition score	2	29	20 to 37
<i>Wool characteristics</i>			
Face covering	2	76	70 to 82
Body folds	1	69	
Neck folds	2	56	54 to 58
Clean fleece weight	2	66	63 to 69
Grease fleece weight	5	46	7 to 74
Staple length	3	71	68 to 75
Resistance to trichostrongyles	2	24	22 to 25

this trait should be effective Yearling body weight is also highly heritable, averaging between 40 and 45 per cent It is also very highly repeatable Heavier yearling ewes also wean heavier lambs and produce heavier fleeces, so selection for this trait would probably be effective and desirable

TYPE AND CONFORMATION

Desirable type and conformation have also received attention in sheep as in other classes of farm animals With this species, however, attention must also be paid to selection for wool production in addition to mutton quality and rate and efficiency of gains

Animals possessing very obvious defects, such as over shot jaws, under-shot jaws, black wool, wool blindness skin folds, shallow bodies, and poor mutton qualities, should be culled from the flock If animals with these defects are eliminated from the breeding flock and selections are made on the basis of body weight and quantity and quality of wool, especially in the selection of rams, perhaps this will be sufficient attention to type

Neale¹³ has successfully used a system of selection and breeding which he calls "corrective mating" Ewes which may be highly productive yet have some objectionable characteristic may be mated to a ram that is especially outstanding in the trait in which the ewes are inferior Many times this corrects the fault in just one cross This is a principle of mating that could be used to improve many traits and is effective, as shown by the history of the development of the many present day breeds of farm animals

CARCASS

We have less information about carcass quality and the degree of heritability of the various carcass items than we have for beef cattle and swine Studies to gain such information are in progress, and results should be available in the near future Since nearly all carcass traits are highly heritable in swine and beef cattle, it seems very likely that the same will also be found to be true in sheep Tenderness and a high proportion of lean to fat in mutton undoubtedly are needed to meet consumer desires

At present, the proportion of leanness and tenderness of mutton can be measured only after the animal is slaughtered, making it impossible to measure this trait in animals to be used for breeding purposes The next best measurement is probably that made in the close relatives of an individual Full sibs are more valuable than half sibs for this measurement, for an individual has twice as many genes in common with full sibs as he has with half sibs Although testing carcass quality in full sibs

is limited to those instances where at least twin births occur, this phenomenon is much more frequent than in beef cattle.

Carcass information may also be obtained on the progeny of a ram, but the same disadvantage of progeny tests applies in sheep as in other classes of farm animals. It takes so long to get a good progeny test that the ram may be dead before his worth is fully known. Once he is progeny-tested, however, and proved to be superior, whether he is dead or living, his offspring should be given preference when selecting breeding animals. If he is dead when the results of progeny tests are fully known, there is still the possibility of keeping the relationship of individuals in the flock closer to the outstanding ancestor through linebreeding.

FLEECE WEIGHT AND QUALITY

The total yearly production of a flock is about 20 per cent from the wool and about 80 per cent from the lambs marketed. This will vary from year to year in different areas and in different flocks where lamb production per ewe is higher than the average. Nevertheless, this shows very clearly that wool production is very important from the economic standpoint.

Wool production is largely dependent upon fleece weight and staple length. In general, for each half-inch that staple length is increased, the weight of the grease wool is increased by three quarters of a pound and clean wool by one-half pound.¹⁸ Greater gains are obtained with increases in staple length in both the fine wool and the coarse wool breeds. With



FIGURE 77 WOOL BLINDNESS IS A TRAIT TO BE AVOIDED. OPEN FACE EWES ARE MORE PRODUCTIVE AND SELECTION FOR THIS TRAIT IS EFFECTIVE (COURTESY OF THE UNIVERSITY OF MISSOURI)

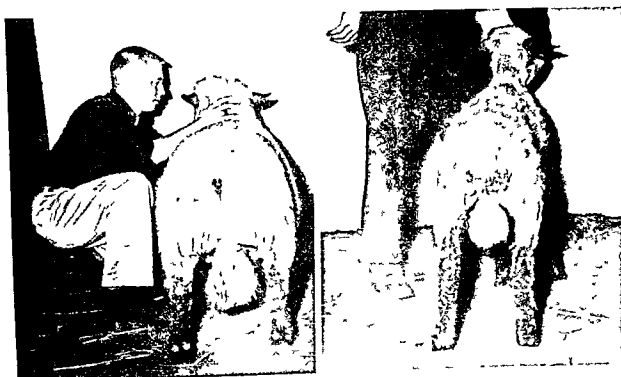


FIGURE 78 A GOOD AND A POOR TYPE RAM. A SIRE SUPPLIES HALF THE INHERITANCE FOR EACH OF HIS OFFSPRING, WHICH MAKES A GOOD ONE OF CONSIDERABLE VALUE. (COURTESY OF THE UNIVERSITY OF MISSOURI)

some breeds, selection may have to be practiced against coarseness of wool, but selection should be practiced for the grade of wool most desirable in a particular area

Heritability estimates presented in Table 48 show that most wool characteristics are highly heritable. The average heritability of fleece weight in nine studies was 47 per cent, and of staple length in eight studies it was 45 per cent. These heritability estimates are high enough that the mating together of the best individuals for these two traits should result in genetic improvement, and because of their economic value, the traits should be given attention in a breeding program.

Face covering in ewes is an important economic trait.¹⁸ Open-faced ewes produce more lambs and wean more pounds of lamb than those with wool-covered faces. In six studies, face covering was 43 per cent heritable, and shows that selection for open faces should be effective. Selection experiments also indicate that this trait can be eliminated in a flock in 10 to 15 years by selection within the group.¹⁸

GENETIC CORRELATIONS AMONG TRAITS

Several studies have been made with sheep to determine the genetic correlations among the economic traits. In general, a large proportion of the same genes seem to be responsible for rapid gains in all phases of the growth period. Thus, there is no antagonism here, and the evidence in-

icates that selection for heavier body weight for any period in life should improve this trait for other periods. Since body weight at all ages seems to be medium to highly heritable, selection for this trait should be effective and very desirable.

Some of the same genes responsible for heavy body weights also seem to cause the production of heavier fleece weight. Although more information on these genetic correlations are needed, it seems that no important genetic antagonism exists between these two traits. Selection for body weight, for instance, should also cause some genetic improvement in fleece weight.

Many of the same genes responsible for greater staple length⁵ are also responsible for heavier fleece weight. Or, at least, the studies do not suggest that there is an important antagonism between these two traits.

INBREEDING IN SHEEP

Results from inbreeding in sheep are very similar to those with other farm animals. Inbreeding in some instances is followed by the appearance of defects that are due to the pairing of recessive genes. In one flock of sheep where inbreeding was practiced for ten years, fifteen blind lambs were born.¹⁵ All traced back to the same sire, and the defect was found to be due to a single pair of autosomal recessive genes. In another study,¹⁶ mild inbreeding for four generations failed to uncover any detrimental recessive factors.

Inbreeding is usually accompanied by a decline in vigor.^{7, 10, 11} Results summarized in Table 49 show that weaning weight and yearling body weight were decreased by three to four pounds for each ten per cent increase in inbreeding. Body score and condition score were not affected adversely.

The weight of wool produced decreased with inbreeding, as did staple length. Possibly this was due to the decline in vigor usually associated with this system of breeding.

CROSSBREEDING IN SHEEP

Crossbreeding has been used in the commercial production of sheep for many years. Since it is so widely practiced, it must have considerable merit. The data presented here on the degree of heterosis for the different traits are based on comparisons of measurements of the various traits in the pure breeds with measurements in their crossbred offspring. Until well-designed experiments have been conducted, heterosis has to be estimated in this way. Very few experiments have been reported in which

TABLE 49

INFLUENCE OF INBREEDING ON VARIOUS ECONOMIC TRAITS
IN SHEEP

Trait	No of reports	Regression coefficient*	
		Average	Range
Weaning weight (lbs)	2	- 0 339	- 0 302 to - 0 375
Yearling body weight (lbs)	5	- 0 381	- 0 055 to - 0 585
Body type score	7	0 010	0 002 to 0 016
Condition score	7	0 007	0 002 to 0 013
Wool characteristics			
Face-covering score	7	0 004	- 0 004 to 0 016
Neck-folds score	7	- 0 003	- 0 009 to 0 001
Clean-fleece weight (lbs)	3	- 0 018	- 0 008 to - 0 025
Grease-fleece weight (lbs)	5	- 0 029	- 0 013 to - 0 057
Staple length (cms)	7	- 0 007	0 000 to - 0 015

*Unit change for one per cent increase in inbreeding

the crossbreds were maintained concurrently with the pure breeds used to produce the cross so that reciprocal crosses could be compared with the pure breeds

Most experiments in crossbreeding of sheep compare the crossbreds with only one of the parent breeds. These are usually comparisons between the offspring of rams of different breeds mated to ewes of a single pure breed and the offspring of purebred rams mated to purebred ewes of that same breed. Average values for the traits from several different studies where comparisons of this kind were made are given in Table 50



FIGURE 79 LAMBS FROM A TWO-BREED CROSS CROSSBREEDING IMPROVES THE HEALTH AND VIGOR OF THE LAMBS RESULTING IN A LARGER PER CENT OF LAMBS BORN WEANED AND FAVORS HEAVIER WEIGHTS (COURTESY OF THE UNIVERSITY OF MISSOURI)

Although these comparisons are not as desirable as those where heterosis could be measured from a comparison of the two pure breeds and their reciprocal crosses produced concurrently, they do give an estimate of the heterosis involved in a two-breed cross where the lambs only were crossbred

Intra uterine survival seems to be improved slightly in crossbred lambs. This is illustrated in the lambs born per ewe, which shows about 3.2 per cent improvement. The greatest improvement from crossbreeding appears to come from increased survival rate from birth to weaning, as shown by 14.6 per cent more crossbred than purebred lambs weaned per ewe that lambled. In these cases, all lambs were produced by purebred dams.

Studies of crossbreeding involving Border Leicester and Romney sheep have been made in New Zealand.² Data obtained to date show very clearly that the crossbreds have an advantage of 20 to 25 per cent over the purebred Romney ewes in the per cent of lambs alive at 28 days per 100 ewes mated. The backcross of the crossbred ewes to Romney rams seems to give inferior results in this respect, as compared to the first-cross ewes. The results of this study, as well as from others, indicate that some breeds produce a considerably larger number of lambs than do others. The over all performance of the crossbred ewes and lambs will be determined to a considerable extent by the prolificacy and mothering ability of ewes from the breeds involved. Thus, crossing two breeds noted for a high percentage lamb crop will give more lambs at weaning than will crossing

two breeds that are known for producing a low percentage lamb crop. Even though the degree of heterosis is the same in both instances, the level of fertility may be considerably different because of the average production of the pure breeds used in the crosses. This is probably also true for other traits.

Crossbreeding increases the weaning weights of lambs by about six to seven per cent and the mature weights of ewes by 10 to 15 per cent over the average of the pure breeds used in the cross. On the same basis, it also increases the weight of wool produced, which could be closely related to increased growth rate and viability of the individuals involved. Staple length was also increased by crossbreeding, but this 30 per cent improvement could be out of proportion to the true heterosis, because some of the experiments summarized in Table 50 were those in which rams of long wool breeds were mated to native ewes or ewes of the short wool breeds.

In general, we must say that more careful experiments are needed that are especially designed to determine the influence of heterosis on the important economic traits in sheep. Most of these traits seem to be improved by crossbreeding, especially the viability of the lambs from birth to weaning.

ment was slightly less than that expected from the amount of selection practiced

Another trait that was used in a selection study was the multi nipple trait in sheep. Usually, ewes have just two nipples, but some have more. Alexander Graham Bell selected for the improvement of this trait in sheep, beginning about 1890.¹⁴ His objective was to develop a type of sheep that would produce two or more lambs and have the milking ability to raise them. He selected for extra nipples with the idea that selection for a large number of nipples would increase the milk supply. It is of interest, however, that in these experiments little or no association was found between increased nipple number and fertility or milk production.

Selection for a larger nipple number was highly effective at first and soon increased the average number in the flock to four. Nipple number seemed to become more or less stabilized at this level, however, and further progress in selection was slow or ineffective, although parents with six nipples were used for breeding purposes. The heritability estimate for nipple number was 14.4 per cent when calculated from the intra-sire regression of the offspring on their dams. This was determined in the population where stabilization of nipple number had already occurred, so perhaps the additive genetic variation for this trait had been exhausted or greatly reduced. Perhaps more than four nipples may have been the result of a combination of genes with nonadditive effects, and this would make mass selection for more than four nipples ineffective.

SELECTION INDEXES

Several indexes may be used for selection purposes, depending upon the goals of the sheep breeder. An index based on the weaning weight of the lamb minus twice its face-covering score might be practical on the farm for some breeds.⁶ For example, if a lamb weighed 55 pounds at weaning and the face score were 3, the index for that lamb would be 55 minus 6 or 49.

An index used for measuring ewe productivity¹⁷ is the weight of the lamb at weaning plus 2.5 times the weight of wool the ewe produces each year, divided by the body weight of the ewe. Where the ewe weighed 100 pounds, weaned twin lambs weighing 90 pounds and produced 8 pounds of wool per year, the index would be $90 + \frac{(2.5 \times 8)}{100} = 1.10$

Still another index, which is more complex and gives considerable weight to wool characteristics is¹⁸

$$\text{Index} = 100 + (1.54 \text{ times clean fleece wt.}) \text{ minus } (1.25 \text{ times staple length in centimeters}) \text{ minus } (0.01 \text{ times body weight in pounds}) \text{ minus } (0.75 \text{ times skin fold score}) \text{ plus } (0.13 \text{ times crimps per inch of wool})$$

BREEDING PLAN FOR SHEEP IMPROVEMENT

The following points are suggested in planning a sheep improvement program

- 1 Identify all individuals in the flock by means of a tattoo ear tag or some other means
- 2 Establish some system of record keeping for all individuals in the flock. (See Figure 80 for sample record forms) Record the performance records on each lamb ewe, and ram

FLOCK RECORD EXAMPLE

No of Ewe _____ Breed _____ Date Born _____

Birth Weight _____ Weaning Weight _____ Yearling Weight _____

Face Covering Score _____

Lambing Record of Ewe

Date Lambed	Sex of Lamb	Birth Weight	Date Weaned	Adjusted Weaning Weight	Weaning Score	Remarks

Wool Record of Ewe

Date Sheared	Weight of Wool	Weight Scoured Wool	Staple length	Wool Grade	Index of Ewe	Remarks

FIGURE 80

- 3 Adjust weaning weights of each lamb for age, sex, for twins, and age of dam where necessary and record these
- 4 Cull ewes that have a poor record of fertility, have obvious defects, or wean light lambs and produce a light fleece at shearing. If desired, a productivity index may be calculated for each ewe in the flock for weaning weight of her lambs and her wool production, and then they may be culled on this basis. Both traits are highly repeatable. Replace ewes with ewe lambs that rank highest on the basis of one of the indexes mentioned earlier, or select those that are superior in body weight, mutton qualities, and wool.
- 5 Where more than one ram is used in the flock, compare the records of their offspring and cull those rams whose offspring are below average for the desired traits. Replace them with ram lambs whose sires and dams have high production records for lambs weaned, mutton type, and heavy wool production. Ram lambs should also be selected on the basis of their own weaning weight, their rate and efficiency of gains after weaning, quality and quantity of wool, and mutton type. Or they could be selected on the basis of an index as was suggested for ewe lambs.
- 6 In commercial lamb production, the use of crossbreeding may be profitable. It would be best to cross those breeds that are both known to be superior in fertility, performance, mutton type, and high quantity and quality of wool.

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Questions and Problems

1. What proportion of the economic value of sheep products is due to wool and to mutton?
2. Is twinning in sheep desirable or undesirable? Can it be improved by selection?
3. The repeatability of weaning weight in sheep is about 43 per cent, whereas the heritability is about 33 per cent. Why this difference?
4. Would you expect to make slow or rapid improvement in selection for most wool characteristics? Explain.
5. Does experimental evidence indicate that it is impossible or difficult to improve fertility, weaning weight, and wool production by selection within the same flock?
6. What would one expect to happen to weaning weights of lambs and grease-fleece weight when full brother and full sister matings are made within the flock?
7. What traits seem to be improved the most by crossbreeding?

- 8 Under what conditions would crossbreeding be recommended?
- 9 Why did selection for increased nipple numbers in the Alexander Graham Bell experiments show rapid progress at first and then stabilize at near four nipples even though parents possessing six nipples were used for breeding purposes?
- 10 Outline in detail the selection and mating procedures you would follow in developing a high quality flock of purebred sheep

Systems of Breeding and ✓ Selection in Dairy Cattle

MORE ATTENTION HAS BEEN GIVEN TO the improvement of performance of dairy cattle through breeding than to any other class of farm animals except poultry. One reason for this is that performance can be measured relatively easily and accurately in this species by weighing the milk produced and by testing for butterfat content at certain intervals during lactation. Another reason is that consumer demands for quality in dairy products are well known, and there has been no need to revise selection objectives over the years as there has been in swine where the demand has shifted from fat hogs to lean hogs in recent years. In addition, there is a fairly constant demand for dairy products throughout the year, since they are so essential for health and they are used daily in most homes throughout the United States.

The same outline will be used in discussing dairy-cattle breeding and selection as was used with swine and beef cattle.

TRAITS OF ECONOMIC IMPORTANCE

The traits of greatest economic importance in dairy-cattle breeding are fertility, milk production, butterfat production, type, and productive life span.

FERTILITY

Normal and regular reproduction in dairy cattle is of great importance, because the lactation period begins when a calf is born. The heritability and repeatability estimates for fertility are very low in dairy cattle, as in beef cattle. This is illustrated by the data summarized in Table 51. These low estimates indicate that most of the variations observed in fertility are

TABLE 51

HERITABILITY AND REPEATABILITY OF FERTILITY IN DAIRY CATTLE*

Fertility Trait	No of reports	Average	Range
<i>Repeatability</i>			
Nonreturn to first service	4	10	3 to 27
Services per conception	2	7	6 to 8
Calving interval	2	7	0 to 13
Time to postpartum estrus	2	9	2 to 15
<i>Heritability</i>			
Nonreturn to first service	3	7	0 to 11
Services per conception	3	-3	-15 to 3
Breeding efficiency**	1	32	
Time to postpartum estrus	2	7	6 to 8

*References 6, 11 12 and 29

**Calving interval as a per cent of 365 days

due to environment and that selection to improve this trait would not be effective. The greatest improvement within a herd would come from proper attention to environmental factors such as nutrition, management, and disease control.

The fact that heritability and repeatability estimates for fertility are low does not mean that genes do not affect this trait. It merely means that the amount of additive genetic variance affecting fertility is small, and it does not discount the possibility that single pairs or at least a small number of pairs of genes with nonadditive effects have an important influence on this trait. For instance, gonadal hypoplasia has been reported to lower fertility in cattle and is thought to be conditioned by a recessive gene.²⁵ Inherited sterility in bulls has been reported in which the sperm is abnormal thus preventing normal fertilization.¹⁹ In addition, inbreeding often causes a decline in fertility that is due to the uncovering of recessive genes¹⁷ or the disruption of a nicking effect due to overdominance and/or epistasis.

MILK AND BUTTERFAT PRODUCTION

Improvement of production of milk and butterfat has received the most attention by breeders through the years. Breeds have been developed which differ significantly in the amount of milk and butterfat they produce. Some breeds produce large amounts of milk with a tendency toward a lower percentage of butterfat, whereas the reverse is true of other breeds. These breed differences strongly suggest a genetic control of both milk and butterfat production.

Heritability and repeatability estimates for milk and butterfat production as well as butterfat percentage are summarized in Table 52. These estimates show that milk and butterfat production are from medium to high in heritability, so that selection for these traits should show improvement. Selection for butterfat percentage should be especially effective, since this trait is between 60 and 65 per cent heritable.

Heritability estimates derived from identical-twin data average considerably higher than estimates calculated from parent-offspring or sib resemblances that measure mostly the variation due to additive gene action but include some that is nonadditive. Heritability estimates based on identical-twin data have been obtained from split-twin and combined identical and fraternal twin records.⁵ Several factors may be responsible for heritability estimates from identical-twin data being higher than those from nontwin data. One explanation is that twins may be more

TABLE 52

HERITABILITY AND REPEATABILITY ESTIMATES FOR MILK AND BUTTERFAT PRODUCTION IN DAIRY CATTLE*

Repeatability	No. of reports	Average	Range
Milk yield	3	53	41 to 64
Butterfat yield	3	42	41 to 43
Butterfat per cent	3	68	59 to 80
Nonfat solids	1	76	

Heritability Based on Parent-Offspring and Sib Resemblance			
Milk yield	30	36	5 to 71
Butterfat yield	17	40	20 to 84
Butterfat per cent	13	62	33 to 83
Persistence of lactation	2	31	27 to 35
Peak milk yield	3	35	14 to 74
Total solids	2	36	34 to 37
Total nonfat solids	2	35	34 to 35
Longevity	1	37	
Type	4	25	14 to 31

Heritability Based on Resemblance Between Identical Twins			
Milk yield	4	89	80 to 90
Butterfat yield	1	86	
Butterfat per cent	2	86	86 to 87
Sugar content	1	60	
Protein content	2	83	78 to 88
Persistence of lactation	1	84	

*Reports in the literature are so numerous that a complete list of references will not be given.

alike than nontwin relatives because their maternal and contemporary environment may be more alike. This would increase the size of the heritability estimates, because members of a pair of twins would resemble each other more closely. In addition, heritability estimates based on identical-twin data may include much of the nonadditive genetic variance, such as dominance and epistasis, in addition to that due to additive gene action, which is not measured to any great extent in nontwin data.

Heritability estimates based on nontwin data would seem to correspond more closely with the realized (or actual) heritability one might obtain in selection under practical conditions. These estimates are still high enough to indicate that mating the best to the best would be the system of choice for improved milk and butterfat production.

Some attention has been given in research to whether heritability estimates are higher in a low-producing or in a high-producing herd. In a study of records of 13,000 cows in Denmark produced by artificial insemination,²⁷ the heritability estimates of milk and fat yields were only slightly greater in cows of a high level of production than in those of a medium level. However, heritability estimates were considerably lower for both traits in cows of a low level of production. No evidence of a herd-sire interaction was found for either trait, with the true ranking of bulls tested on cows of a low, medium, or high level of production being the same in each case. It was concluded that selecting bulls on the basis of their daughters' records in a higher yielding herd would be preferred in testing bulls for use in artificial insemination. A similar study in Sweden²¹ showed that heritability and repeatability of milk yield and butterfat percentage were only slightly higher in high- than in low-producing herds. These two studies suggest that selection or progeny-testing in herds of medium-to-high production would be preferred, although the advantage is small.

MEASUREMENT OF MILK AND BUTTERFAT PRODUCTION

Several nongenetic factors are known to cause variations in the production records of dairy cattle. Adjusting records for factors known to cause variations would make selection more effective, because the superior animals would then be more likely to be superior because of inheritance. Some of these factors may be corrected for by recording production for a standard length of time or by using adjustment factors derived from a large body of data from many animals.

The Dairy-Herd-Improvement-Association²³ recommends that records of production be adjusted for length of lactation period, for number of milkings per day, and for age of the cows when they produce the records. Adjustments of records for these variables are necessary for a more valid comparison of sires as well as dams for selection and herd improvement

programs Several of the breed associations have correction factors of their own, but those presented here are recommended for standardizing Dairy Herd Improvement Association records in proving sires

Lactation records are usually reported on a 305 day basis, because this reduces the variation in production records caused by varying lengths of lactation and because pregnancy has little or no influence on production during a lactation period of this length This lactation period is also more desirable, because cows should calve each year and should have a dry period between two successive lactations

Several methods of estimating 305 day milk and butterfat yield have been used in place of weighing and testing the milk at each milking One method is to make monthly measurements of milk production and percentage of butterfat and then multiply these figures by the number of days the cows are milked during the month Another method is to sum the first ten testing day values taken at approximately monthly intervals, and multiply this figure by 30.5 to estimate the 305 day lactation yield²⁸ Each cow tested must have calved six or more days previous to the date of testing, but no correction is made for date of calving Most methods used are fairly accurate, since they are highly correlated with each other and with actual yields of milk and butterfat

Milk yield records are sometimes taken for 365 days rather than for the shorter period of 305 days These records may be adjusted to a 305 day basis by multiplying by the factor 0.85

The age of the cow also has an important influence on the amount of milk she produces Two and three year old cows are considerably below their peak production, which they should reach at six to eight years of age After nine years of age, cows gradually decline in production Since age is such an important source of variation in milk and butterfat yield, conversion factors are used to convert records to a 'mature equivalent' basis This means that records are adjusted to an age at which cows of the breed show their maximum production Age conversion factors for 305 day production records are given in Table 53 for the different breeds of dairy cows To illustrate how these factors may be used, let us assume that the 305 day lactation record of an Ayreshire cow that is 3.5 years of age is 5,000 pounds of milk To convert this to a 'mature equivalent' basis we multiply this by the factor 1.13 found in Table 53 The adjusted record would be 5,650 pounds of milk Age adjustment factors for cows of other breeds are also presented in this table²⁸

The number of times cows are milked per day is also an important source of variation in milk production More frequent milkings result in the production of more milk and therefore comparisons between cows, some of which were milked twice daily and others three or four times daily, are not valid Since most cows are milked only two times per day, records are usually adjusted to this basis by conversion factors presented

TABLE 53

DAIRY-HERD-IMPROVEMENT ASSOCIATION AGE-CONVERSION FACTORS
FOR 305-DAY PRODUCTION RECORDS

Age in years	Ayreshire	Brown Swiss	Guernsey	Holstein; Red Dane	Jersey	Red Poll, M. Shorthorn	Mixed Breeds
2.0	1.30	1.45	1.24	1.31	1.27	1.42	1.31
2.5	1.24	1.35	1.18	1.24	1.21	1.30	1.24
3.0	1.18	1.23	1.12	1.18	1.15	1.24	1.18
3.5	1.13	1.16	1.08	1.12	1.09	1.18	1.12
4.0	1.10	1.10	1.06	1.08	1.06	1.13	1.08
4.5	1.07	1.07	1.04	1.04	1.03	1.10	1.04
5.0	1.03	1.04	1.02	1.02	1.02	1.07	1.02
5.5	1.02	1.02	1.01	1.02	1.01	1.05	1.02
6.0	1.00	1.00	1.00	1.01	1.00	1.01	1.00
6.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7.0	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7.5	1.00	1.00	1.01	1.00	1.01	1.00	1.00
8.0	1.00	1.00	1.01	1.00	1.01	1.01	1.00
8.5	1.01	1.01	1.02	1.01	1.02	1.01	1.01
9.0	1.02	1.01	1.02	1.02	1.02	1.02	1.02
9.5	1.02	1.02	1.03	1.03	1.03	1.03	1.03
10.0	1.03	1.02	1.04	1.04	1.04	1.04	1.04
10.5	1.03	1.03	1.05	1.05	1.05	1.05	1.05
11.0	1.04	1.04	1.06	1.06	1.06	1.06	1.06
11.5	1.05	1.05	1.07	1.07	1.07	1.07	1.07
12.0	1.06	1.06	1.08	1.09	1.08	1.08	1.08
12.5	1.07	1.07	1.09	1.10	1.09	1.09	1.09
13.0	1.07	1.08	1.10	1.12	1.10	1.10	1.10
13.5	1.08	1.09	1.11	1.13	1.11	1.11	1.11

Adapted from USDAP ARS-S2-1, January 1955

in Table 54 This correction is made after adjustments are made to a 305-day "mature equivalent" basis

Since breeds of dairy cattle differ in the amount of milk they give and in butterfat percentage, yields are sometimes reported on a four per cent fat-corrected milk basis The formula for this conversion is:

$$\text{Fat-corrected milk (4 per cent milk)} = (0.4 \times \text{milk}) + (15 \times \text{fat})$$

For example, if a cow produced 12,000 pounds of 3.5 per cent milk containing 420 pounds of fat, her four per cent-equivalent record would be

$$\begin{aligned} \text{Fat-corrected milk} &= (12,000 \times 0.4) + (420 \times 15) \\ &= 4800 \quad + 6300 \\ &= 11,100 \text{ lbs} \end{aligned}$$

TABLE 54

FACTORS FOR REDUCING 305-DAY, AGE-CORRECTED RECORDS TO A
TWICE-A-DAY MILKING BASIS

Number of days milked	Factor for 3-times-a-day milkng			Factor for 4-times-a-day milkng		
	2 to 3 years of age	3 to 4 years of age	4 years of age and over	2 to 3 years of age	3 to 4 years of age	4 years of age and over
5 to 15	0.99	0.99	0.99	0.98	0.99	0.99
16 to 25	0.98	0.99	0.99	0.97	0.98	0.98
26 to 35	0.98	0.98	0.98	0.96	0.97	0.97
36 to 45	0.97	0.98	0.98	0.95	0.96	0.96
46 to 55	0.97	0.97	0.97	0.94	0.95	0.96
56 to 65	0.96	0.97	0.97	0.93	0.94	0.95
66 to 75	0.95	0.96	0.96	0.92	0.93	0.94
76 to 85	0.95	0.95	0.96	0.91	0.92	0.93
86 to 95	0.94	0.95	0.96	0.90	0.91	0.93
96 to 105	0.94	0.94	0.95	0.89	0.91	0.92
106 to 115	0.93	0.94	0.95	0.88	0.90	0.91
116 to 125	0.92	0.93	0.94	0.87	0.89	0.90
126 to 135	0.92	0.93	0.94	0.87	0.88	0.90
136 to 145	0.91	0.93	0.93	0.86	0.88	0.89
146 to 155	0.91	0.92	0.93	0.85	0.87	0.88
156 to 165	0.90	0.92	0.93	0.84	0.86	0.88
166 to 175	0.90	0.91	0.92	0.83	0.85	0.87
176 to 185	0.89	0.91	0.92	0.82	0.85	0.86
186 to 195	0.89	0.90	0.91	0.82	0.84	0.86
196 to 205	0.88	0.90	0.91	0.81	0.83	0.85
206 to 215	0.88	0.89	0.90	0.80	0.83	0.85
216 to 225	0.87	0.89	0.90	0.79	0.82	0.84
226 to 235	0.87	0.88	0.90	0.79	0.81	0.83
236 to 245	0.86	0.88	0.89	0.78	0.81	0.83
246 to 255	0.86	0.88	0.89	0.77	0.80	0.82
256 to 265	0.85	0.87	0.88	0.77	0.79	0.82
266 to 275	0.85	0.87	0.88	0.76	0.79	0.81
276 to 285	0.84	0.86	0.88	0.75	0.78	0.80
286 to 295	0.84	0.86	0.87	0.75	0.78	0.80
296 to 305	0.83	0.85	0.87	0.74	0.77	0.79

From USDAP ARS-52-1, January 1955.

PRODUCTIVE LIFE SPAN IN DAIRY CATTLE

This is another trait of economic importance. A study of 101 commercial dairy herds in Florida⁴ showed that the average productive life of dairy cows in a herd maintained mostly by purchased replacements was 3.9 years after entering the herd at two years of age. In 14 herds where replacements were home raised, this figure increased to 4.7 years. The reasons for the disposal of 58 per cent of 2,182 cows in these herds were udder trouble, low production, and reproductive disorders.

In a New Jersey study,⁴³ longevity in a Holstein-Friesian herd was found to be about 37 per cent heritable, as calculated from the intra-sire regression of daughters on dams. Breeding efficiency, expressed as a percentage derived from the actual calving interval in days to the ideal of 365 days, was 32 per cent heritable. The association between productive life span and breeding efficiency was low and insignificant.

TYPE AND CONFORMATION

Type in dairy cattle has received much attention both in the show-ring and from breeders in selecting replacement animals. As shown in Table 52, type in dairy cattle is about 25 per cent heritable, which indicates that only moderate progress could be made in selection for the improvement of this trait.

Type and conformation are valuable because superiority in these traits should help the animal to maintain a long and highly productive life. The desirable items are size and development of the mammary gland, proper placement of the teats, soundness of feet and legs, and body capacity, which should give some indication of the animal's ability to consume large amounts of grains and roughages.

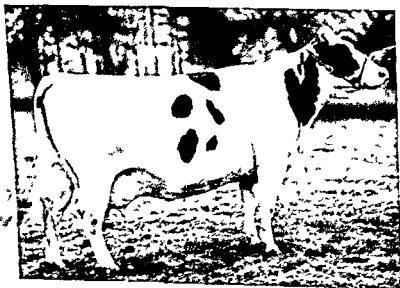


FIGURE 81 PRINCESS BREEZEWOOD R A PATSY 3816059 (VG) IS ONE OF THOSE INDIVIDUALS THAT HAVE GOOD TYPE AS WELL AS PERFORMANCE. HER RECORD WAS 36,821 POUNDS OF MILK AND 1866 POUNDS OF BUTTER-FAT AT FIVE YEARS OF AGE. (COURTESY OF THE HOLSTEIN-FRIESIAN ASSOCIATION OF AMERICA.)

Differences between dairy- and beef-cattle type are very obvious. In a general way, there is a relationship between body form and milk production in dairy cattle, but within a herd or breed the relationship seems to be relatively small. Most studies between dairy type and production show a positive but low phenotypic correlation between these traits. The genetic correlations are also very low, which indicates that selection for type alone would result in little improvement in production. The two traits seem to be inherited independently, and to improve both, selection for both must be practiced.

GENETIC CORRELATIONS BETWEEN PRODUCTION TRAITS

Genetic correlations between the various traits in dairy cattle are summarized in Table 55. The data indicate very clearly that there is a strong genetic correlation between milk yield and butterfat yield, with an average value of 0.81. Thus, many of the same genes affect both traits, and intensive selection for one should bring about improvement in the other. This is a desirable correlation since it is positive. The genetic correlation between milk yield and butterfat percentage was negative in all studies and averaged -0.41 . This suggests that many of the genes responsible for high milk yields cause the production of a lower percentage of fat in the milk. These figures seem to be borne out by the association of the two traits seen in the different breeds of dairy cattle. Holstein-Friesians, for instance, give large amounts of milk but a lower butterfat percentage. Jerseys give a smaller amount of milk, and the percentage of butterfat is much higher. This negative genetic association is not of great economic importance, because most dairymen are probably more interested in the total fat and milk yield than they are in the percentage of fat in the milk.

The data presented in Table 55 show that there is a very low genetic correlation between fat yield and fat per cent in the milk. This means

TABLE 55

GENETIC CORRELATIONS BETWEEN TRAITS IN DAIRY CATTLE

<i>Traits correlated</i>	<i>No. of studies</i>	<i>Average</i>	<i>Range</i>
Type and butterfat yield	3	-0.15	-0.52 to 0.08
Type and milk yield	3	0.05	0.00 to 0.08
Milk yield and butterfat per cent	7	-0.43	-0.58 to -0.20
Milk yield and butterfat yield	6	0.81	0.62 to 0.92
Fat yield and fat per cent	3	0.14	-0.03 to 0.26

that very few of the same genes affect these two traits and selection for one should not cause a genetic change in the other

SELECTION OF DAIRY SIRES

Since milk production is limited to only one sex, sires must be selected for performance on the basis of the records of their female relatives, including their dams sisters and daughters. The recognition of the importance of dairy sire selection has resulted in many studies of this problem.

The old adage that the bull is half the herd applies to the breeding of dairy cattle, but probably needs more attention now than a few years ago. The reason for this is that through the use of artificial insemination the bull may supply half the inheritance for many calves in many herds.

A bull cannot be fully progeny tested until his daughters complete their first lactation period. This means that some system must be used for the selection of young bulls that will be progeny tested later in their lives. The best procedure for selecting a young sire is to retain one whose sire is progeny tested, whose dam is of known high productivity, and whose family is also noted for its high productivity. In addition, attention should be given to the productivity of his female collateral relatives. In a study of records to determine the best method of selecting a young bull,¹³ it was found that more reliance could be placed on the average production of the paternal half sisters of a bull than on that of the dams of his paternal half sisters or the production records of the paternal half sisters of the bull's dam. The average production of the bull's own dam or that of his maternal half sisters showed no relationship to his daughters' production.

Great emphasis has been placed on the use of progeny tested dairy sires for breeding purposes. Many systems of indexing dairy bulls have been proposed. The equal parent index has been used in the past. It is relatively simple to calculate but has proved inaccurate in natural service for bulls evaluated by this method do not repeat their index when used for artificial insemination. This index is based on the theory that the progeny should average midway between the two parents. It is usually calculated by finding the differences between the average milk yield and butterfat test of a group of cows and the averages for their daughters out of a particular bull. If the daughters' average production exceeds that of the dams, the difference is added to the daughters' record to get the equal parent index for the bull. If the daughters' average production is less than that of the dams, the difference is subtracted from the daughters' average to secure the bull's index. Thus, this index always places the daughters' average midway between the dams' actual average and the

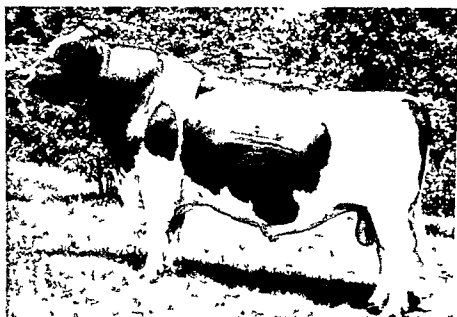


FIGURE 82 WIS CAPTAIN (1738) A Gold Medal Proved Sire THIRTEEN PAIRS OF DAUGHTER DAM COMPARISONS SHOWED A DIFFERENCE OF +1350 POUNDS OF MILK AND 56 POUNDS OF BUTTERFAT IN FAVOR OF THE DAUGHTERS IN FOUR YEARS HE PERFORMED 219 043 SERVICES BY ARTIFICIAL INSEMINATION WITH APPROXIMATELY 145,000 OFFSPRING AT THAT TIME HE WAS STILL GOING STRONG AS A SIRE (COURTESY OF THE AMERICAN BREEDERS SERVICE, CHICAGO, ILLINOIS)

bull's "equal parent index" In computing the index, the records are adjusted to a 305 day, 2 times, mature equivalent basis The index is calculated for milk yield, per cent butterfat, and fat yield

Another method of progeny testing bulls is to compare the average of a bull's daughters with that of their dams This comparison is made after the dams' and the daughters' records have been adjusted to a 305 day, 2 times, mature equivalent basis If any of the dams or the daughters have more than one record, these records are averaged before the comparison is made For progeny tests to be of value, the environmental conditions should be as nearly the same as possible for both the daughters and the dams In addition, daughters tested should be a random sample of those from a particular sire and should not be selected because they have a higher potential level of production, with those of a lower potential being left out of the comparison Such a procedure would cause one to over estimate the inherent production level transmitted by the bull

Studies of the number of daughters necessary to progeny test a sire by means of natural service indicate that very little accuracy is added by testing more than eight to ten daughters Some accuracy is added with larger numbers of daughters, but the accuracy per additional daughter decreases as the number of daughters tested increases However, the use of larger numbers of daughters is more practical when artificial insemination is used

RESULTS OF SELECTION IN DAIRY CATTLE

Definite breed differences in milk and butterfat production leave little doubt that selection for these traits has been effective. Nevertheless, very few well controlled selection experiments with dairy cattle have been reported.

In a U S D A study,⁹ a Holstein herd was established in 1918 and a selection study was initiated. No females were culled until after they completed at least one lactation record. Environmental conditions were kept as constant as possible throughout the experiments. Ten proved sires were used during a period of 28 years. Sires were used whose unselected daughters were uniformly high producers and produced better than their dams.

The average yearly production of 16 foundation cows was 17,524 pounds of milk and 601 pounds of butterfat. This was a high level of production. The average production of 183 unselected daughters that were descendants of the ten sires was 17,491 pounds of milk and 629 pounds of butterfat. Some of the proved sires improved the average of their daughters' records over their dams whereas others lowered them. The last three progeny-tested sires used produced unselected daughters whose milk production records ranged between 18,680 and 19,850 pounds of milk and between 683 and 711 pounds of butterfat. This study showed conclusively that superior, progeny tested bulls were hard to find.

To make genetic improvement, genetically superior animals must be used. Since males have more progeny than females, they may be tested more thoroughly, and genetic improvement can best be made by using those that are genetically superior. Artificial insemination increases the possibility of making more use of superior progeny tested sires. In 1939, the average number of services per sire in artificial insemination was 228, according to U S D A figures. This has steadily increased, so that at the present time about 2500 services are made per sire per year, and between six and seven million cows are inseminated each year.

Several reports in the literature have attempted to assess the progress made by using artificial insemination in dairy herds.^{18 33 42} Usually records of performance of cows produced by this method are compared with those of cows produced by natural matings in the same herd at the same time. Cows from artificial insemination have proved to be significantly superior in production in some instances.

INBREEDING IN DAIRY CATTLE

Many experiments have been conducted with inbreeding in dairy cattle. The main objective of the experiments in most studies was to

determine if pure lines could be formed in which individuals had a level of production as high as that of outbred animals. In addition, it was desired to learn what the effects of inbreeding might be in this class of farm animals.

OCCURRENCE OF DETRIMENTAL GENES

Several experiments have clearly shown that inbreeding in dairy cattle uncovers recessive genes if they are present in the foundation stock. A study of genetic and environmental factors in the development of the American Red Danish cattle³⁰ showed that 65 calves in 27 herds were born with paralyzed hind quarters. Forty-two calves in 11 herds were dead at birth and showed ankylosis and mummification. These defects are inherited, and they have been reported in Denmark. Both defects were traced to certain bulls of the breed. A gene frequency analysis showed that about 25 per cent of American Red Danish cattle were heterozygous for the paralyzed condition and 11 per cent were heterozygous for ankylosis.

In a study conducted in California,³¹ an increase in calf mortality that accompanied inbreeding was partly accounted for by two lethal genes, one of which controlled an anomaly of the liver and the other an anomaly of the heart. Neither of these defects could be determined by their external morphological appearance. In a U.S.D.A. study of inbreeding,⁴⁴ a few Guernsey calves were deformed at birth, and apparently a recessive gene was involved. In an inbreeding experiment at the New Jersey station,² data on four foundation herd sires were studied. As inbreeding progressed, some of the descendants of one bull died at birth or shortly afterward of an inherited defect called 'Bulldog'. Various abnormalities of the reproductive tracts also occurred, and this sire family had to be abandoned. Another sire produced offspring that were undesirable and many of which also carried a factor for red spotting of the hair coat. Apparently, two of the four sires transmitted no apparent genetic defect, and one of these produced descendants of very satisfactory types and performance.

It is apparent from the literature that dairy cattle may carry several recessive genes that are uncovered by inbreeding. Most of these defects in the heterozygous state cannot be recognized by the morphological appearance of the individual and can be discovered only by an appropriate progeny test. Thus, any breeder who practices inbreeding risks an increase in the occurrence of genetic defects in his herd. The only sure way to determine if the breeding animals are carrying such genetic defects is to inbreed and progeny test them. This takes time and is costly, but there are probably some sires of outstanding genetic merit that do not carry lethal or detrimental genes and that should be identified.

EFFECT OF INBREEDING ON GROWTH

Results of experiments do not all agree as to the effect of inbreeding on growth rate. In general, however, inbreeding seems to decrease birth weight and mature weight.^{1,10 28 30 34,44} In one study,²⁸ it was found that inbreeding slowed the growth rate early in life but permitted the later rapid growth to continue longer so that mature size was not decreased but may have even been increased. At the New Jersey Station,²⁸ Holstein-Friesians were inbred up to 20 per cent without any decrease in weight at maturity as compared to outbred animals. When inbreeding was more than 20 per cent, inbred females grew normally to approximately first calving age, then developed more slowly thereafter.

EFFECTS OF INBREEDING ON FERTILITY

Inbreeding did not cause an increase in the number of services per conception in grade Holsteins⁴⁴ and seemed to cause little or no increase in abortions and stillbirths. However, in most experiments, an increase in inbreeding has resulted in an increase in calf mortality after birth. Part, but not all, of this increased mortality was due to lethal factors. Apparently, inbred calves were less able than outbreds to cope with environmental conditions during this stage of life.

EFFECTS OF INBREEDING ON PRODUCTION

Some of the early experiments on inbreeding in dairy cattle did not report the coefficients of regression for milk and butterfat production on inbreeding as calculated from Wright's coefficient of inbreeding. Results of later studies which reported such figures are summarized in Table 56. In some experiments, inbreeding seemed to result in an increase in production^{2,3,44} but, in general, this was not true. At the New Jersey Station³

TABLE 56

EFFECTS OF INBREEDING ON MILK AND BUTTERFAT PRODUCTION

Production trait	No of reports	Regression coefficient*	
		Average	Range
Pounds of milk	4	- 71.900	- 209.800 to - 0.074
Per cent of butterfat	2	0.006	0.003 to 0.008
Pounds of butterfat	4	- 2.310	- 4.880 to - 0.300

*Decrease or increase for each 1 per cent inbreeding

References 24, 36, 40, and 41



FIGURE 83 A CALF AFFECTED BY A RECESSIVE LETHAL GENE WHICH CAUSES PREGNANCY TO BE PROLONGED IN SOME CASES AS LONG AS 60 TO 70 DAYS WITH A BIRTH WEIGHT OF UP TO 150 TO 160 POUNDS. THE CALVES HAVE TO BE DELIVERED BY CAESARIAN SECTION IN SOME CASES. (COURTESY OF DR. L. W. HOLM, SCHOOL OF VETERINARY MEDICINE, UNIVERSITY OF CALIFORNIA, DAVIS, CALIFORNIA.)

experimental results indicated that inbreeding up to 20 per cent, accompanied by rigid selection, could result in superior animals. It was concluded that the primary results of the inbreeding work at that station was the development of superior inbred sires with a marked prepotency for desirable growth, type, butterfat test, and production.

CONCLUSIONS ON INBREEDING

Results of inbreeding work in dairy cattle show that inbreeding is often detrimental, as measured by the increased occurrence of recessive defects, greater calf mortality, and lowered production of milk and butterfat in inbred cows. Nevertheless, adverse effects have not always been observed. Certain inbred sires and dams seem to be very prepotent for high production. This suggests that a linebreeding program using outstanding animals within the breed could develop outstanding lines. The development of several such lines within a breed could produce some very superior animals if the best lines were crossed. The heritability of the traits suggests that additive genes have a moderate-to-great effect on production, whereas inbreeding and crossbreeding effects are only moderate. This would suggest that selection of high-producing stock and fixing the desired traits by moderate inbreeding would be of value in a dairy-cattle breeding program.

CROSSBREEDING IN DAIRY CATTLE

Results of experiments in which the performance of the F_1 crossbreds is compared with that of the average of the two parent breeds are sum-

Table 57

INFLUENCE OF CROSSBREEDING ON MILK PRODUCTION
IN DAIRY CATTLE

Breeds crossed	<i>F₁ as per cent of P₁ average</i>		
	<i>Lbs milk</i>	<i>%fat</i>	<i>Lbs fat</i>
Red Danish × Jersey	103	98	104
Friesian × Guernsey	107	97	109
Friesian × Jersey	112	115	137
Jersey × Angus	96	96	90
Friesian × Angus	98	97	98
Average	103	101	108

References 7 8 14 32 45 and 46

marized in Table 57. In some of these experiments numbers of animals involved are small but they still give some indication of the effects of heterosis on milk and butterfat production.

Results indicate that there is some heterotic advantage in milk and butterfat yield with little or no advantage for the percentage of butterfat in the milk. In three experiments involving crosses of the dairy breeds from 3 to 12 per cent heterosis was observed in milk yield and from 4 to 37 per cent in fat yield. This means that there was a tendency for the F_1 average to be closer to the average of the more productive breed. It should be pointed out however that in none of the studies did the average of milk production by the F_1 crossbreds exceed that of the more productive parent breed.

In the crosses of the dairy breeds the average butterfat yield of the F_1 crossbreds exceeded that of either parental breed in two out of three experiments. In two of the three reported experiments the percentage of butterfat in the milk of the F_1 crossbreds was slightly lower than that of the average of the parental breeds. This trait shows that heterosis effects were slight or even slightly negative. In none of the three experiments did the average percentage of butterfat in the milk of the crossbreds exceed that of the most productive parent.

TABLE 58

RESULTS OF CROSSBREEDING EXPERIMENTS WITH DAIRY CATTLE AT BELTSVILLE, MARYLAND*

Groups tested	No of cows	Mature-Equivalent Values		
		Lbs milk	% fat	Lbs fat
Foundation purebreds	55	13,799 (100)	4.30 (100)	594 (100)
2-breed crosses	55	17,811 (129)	4.49 (104)	799 (135)
3-breed crosses	58	18,240 (132)	4.39 (102)	801 (135)

*Adapted from USDATB 1074 1954 Figures in parentheses are production figures as a per cent of the foundation purebreds, or an estimate of heterosis

experiment was initiated in 1939 with foundation cattle from the Holstein-Friesian, Guernsey, Jersey, and Red Danish breeds. These cows were mated in rotation to proven sires of the Holstein-Friesian, Jersey, and Red Danish breeds. All production records of crossbred females and their foundation dams, except the Red Danish dams, were made on the basis of three times per day milking for a 365 day lactation period. In this experiment, there was a considerable advantage of the two breed crosses over the foundation purebreds in milk and butterfat yield and, to a lesser extent, in the percentage of butterfat. The three breed cross had only a slight advantage over the two breed crosses. Crossbred cows had a higher degree of persistency of production than purebreds, which accounted for a part of their higher level of production.

In the Beltsville experiment, the average of the crossbreds exceeded or equalled the average of any of the parental foundation breeds on a mature equivalent basis. This experiment shows a higher degree of heterosis for milk and fat yield than other experiments reported in Table 57.

CONCLUSIONS ON CROSSBREEDING IN DAIRY CATTLE

More experimental results are needed to assess properly the value of crossbreeding in dairy cattle production. From the standpoint of milk and fat yield, the results to date indicate that selection for high performance within the existing breeds might be preferred to crossbreeding. Some established breeds are noted for high milk yield, whereas others are noted for the production of a high percentage of butterfat, which gives a creamy, yellow color to the milk. Keeping a herd containing cows of the two breeds and mixing the milk for sale purposes perhaps would be more advantageous to the dairyman than crossbreeding. On the other hand, where a dairyman has a herd whose production is average or below,

crossbreeding might be of some advantage. In such a case the transmitted high productivity of the sire used would be more important than the breed to which he belongs.

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Questions and Problems

- 1 What are the most effective ways to improve fertility or breeding efficiency of a dairy herd?
2. What evidence do we have that the same genes affect milk and butter fat production?

- 3 Why are heritability estimates calculated from identical twin data higher than those calculated from the regression of daughters on dams?
- 4 Milk yield is about 53 per cent repeatable and 36 per cent heritable. Why the difference between these two estimates?
- 5 Could genetically superior individuals be identified more accurately in a low producing or a high producing herd?
- 6 In culling cows, what adjustments should be made before cows are compared?
- 7 A cow produces 14 000 pounds of 3.2 per cent milk in a 305 day lactation period. What is the production of this cow on the basis of 4 per cent fat corrected milk?
- 8 A two year-old Holstein heifer makes a record of 10 000 pounds of four per cent milk in 340 days when milked three times per day. What is her record adjusted to a mature equivalent 305 day, two times a day milking basis?
- 9 Is type and conformation of any importance in selection for superior milk and butterfat production? Explain.
- 10 A group of cows produce an average of 8 500 pounds of milk on a mature equivalent 305 day, two times a day milking basis. Their daughters out of a particular bull average 9 000 pounds on the same basis. What is the equal parent index of the bull?
- 11 What traits are affected the most by inbreeding in dairy cattle?
- 12 Would you recommend crossbreeding in dairy cattle? Discuss some of the advantages and disadvantages of this system of mating.

26

Systems of Breeding and Selection in Horses

INCREASED MECHANIZATION HAS RESULTED in a gradual decline in numbers of draft horses and mules on the farm. Mechanization has become so complete in recent years that it is an oddity to see a farmer doing field work with anything but a tractor. The decline in the need for draft animals has resulted in less interest in research on breeding and improvement of these animals. In fact, many recent textbooks on breeding, feeding, and management of the different species of farm animals include no chapters on horses and mules; many colleges have eliminated a study of horse and mule production methods from their animal husbandry curricula.

Although horses have decreased in number in recent years, they have not been completely forgotten. Many people still love to ride, and many stables are maintained for this purpose. The breeding and training of Thoroughbreds, Standardbreds, and Quarter horses is a highly specialized business, and outstanding animals are valued at many thousands of dollars. Harness racing still has its place at many state fairs during the summer, and there are many who breed horses especially for this purpose. Quarter horses are also bred for their racing ability, as well as for their beauty and their ability to work cattle on the range. Although many cowboys ride the range in jeeps and pickup trucks, many still take their favorite cow ponies along in trailers or trucks so they can work cattle on horseback where machines cannot go.

The cowboy and his cow pony will never completely disappear from the western range. If they did, it would be a tragic loss to this country. The trust and mutual understanding between a cowhand and his favorite cow pony is something to behold. The author can speak from personal experience in this respect, since he spent several years in the range country and many pleasant hours, and even days, on horseback working cattle in Arizona.

No attempt will be made in this chapter to outline genetic principles specifically involved in breeding a particular type of horse. The discussion will be limited to the inheritance of those traits that are of the greatest economic importance.

TRAITS OF ECONOMIC IMPORTANCE

FERTILITY

Lowered fertility of the brood mare is as serious a problem as it is in any class of farm animals. A study of 45 draft and 35 light mares during two breeding seasons showed that only 69 per cent conceived and produced foals.¹ This low percentage colt crop seems to be similar to that obtained all over the United States. Perhaps one reason for the decreased breeding efficiency in mares is the extreme length of the estrus period, which averages between five and six days. Ovulation, as a general rule, occurs one to two days before the end of estrus. The time of mating in relation to the time of ovulation in the mare is of great importance because of the limited life of both spermatozoa and ovum in the female reproductive tract. If the spermatozoa are introduced into the female reproductive tract too long before or too long after the release of the ovum from the ovary, they may die and fail to fertilize the egg.

The heritability of fertility in horses is low, and one report in the literature gives a heritability estimate of five per cent.² This low estimate seems reasonable, since fertility is also lowly heritable in other species of farm animals. Selection for improved fertility in horses would probably be ineffective. Attention to the improvement of fertility through such environmental factors as nutrition, management, and disease control is indicated. In management practices, treatment for certain pathological and/or functional disorders responsible for lowered fertility or sterility could be of value, providing such abnormalities are not inherited. Much work has been done in this area in the past several years.

PERFORMANCE

Horses have been bred for many different purposes, and their ability to do the task for which they were bred has been an important factor in their popularity. The several different aspects of performance will be discussed separately.

Racing ability This trait depends probably upon certain physiological and nervous qualities of the individual as well as upon its anatomical structure. Since so many different factors are involved, it seems very probable that the trait is influenced by the action and interaction of many genes. Breeders believe that racing ability is highly heritable, and they

are willing to pay very high prices for an outstanding stallion or even thousands of dollars for his services

Several schemes have been used to measure the racing ability of Thoroughbreds. The average earning index has been used by several investigators.³ This index is computed by first calculating the average amount of money earned by the breed each year, this is determined by dividing the total amount of earnings for all animals by the total number of starters. The earnings of a horse are then compared with the average for the breed for that year. A horse that wins exactly as much money as the average is given an adjustment factor of 1.0. A horse that wins four times the average of the breed has an adjustment factor of 4.0. This adjustment factor is figured for each year that the horse is raced, the factors summed and then divided by the number of years raced. The resulting figure is the average earnings index.

Studies of the relationship of stake winners to the earnings index of their dam⁴ indicate that this trait is highly heritable. Thus, mares with the higher earnings index would have the higher racing ability. The earnings of the offspring of mares with higher indexes were also higher than those of the offspring of mares with lower indexes.

A heritability estimate of 60 per cent for racing ability was found in a study at the Kentucky Agricultural Experiment Station.⁵ This study, together with other evidence, indicates that racing ability is highly heritable and is influenced by many genes with additive effects. The heritability, however, may not be as high as indicated here.

Racing ability in the Standardbreds and Quarter horses has not been studied in detail from the genetic standpoint, but the beliefs of breeders that this trait runs in certain families and that certain sires produce better performing offspring than others indicates that this trait is highly heritable. Speed on the track varies in different individuals. Some horses can run very fast for a short distance, after which they falter. Others can maintain a rapid pace for much longer distances. This 'staying' ability must also be heritable, since the breeds or types differ in this respect, the Thoroughbred being noted for racing ability at the longer distances and the Quarter horse at the short distance of a quarter mile.

Trotters and pacers The ability to trot or pace definitely depends upon the genotype of the individual. The trotting gait has been reported to be due to a dominant gene, whereas the pacing gait is due to the recessive gene. Natural pacers under this mode of inheritance would breed true and would be homozygous for the recessive gene. It is possible to teach a trotter to pace, but the natural inclination to trot or pace seems to be inherited in a simple Mendelian manner.

Speed in trotting and pacing could be influenced by several pairs of genes, many of which act in an additive manner. As far as is known, no

actual heritability estimates for speed in trotting or pacing have been published.

Cow sense The term "cow sense" as used here refers to the ability or aptitude of the horse to understand and work cattle. In working cattle, a cow pony has several different jobs to do; often, different horses are used for different jobs. One is to carry his rider over the range to round up cattle in an area of several sections. The range covered is often rocky and brushy, and the pony must have stamina and surefootedness. Another job, mostly limited to specially rough areas where cattle are sometimes wild, is to carry the rider close enough to a running steer so that it can be roped. In the rodeo, cow ponies must be fast enough to catch a speeding calf and then must keep the rope taut when the calf is caught so the cowboy can make a quick tie. Still another job is reserved for the "cutting" horse, who must have the agility and the cow sense to cut a single animal from a herd with very little guidance by the rider. Although considerable training is necessary to make a good roping or cutting horse, training alone is not sufficient.

Little or no research has been done to determine if these traits are inherited. Some horses seem to have "cow sense"—others do not. Cow men have long been of the opinion that cow sense is inherited. In many cases they will travel long distances and pay high prices to get a colt from a particular line of breeding or out of a particular stallion.

Type and conformation Within certain broad limits, proper type and conformation are necessary for the individual to excel in performance. A Thoroughbred built like a draft horse would not be expected to be a stakes winner. Similarly, draft type is avoided in selecting and breeding cow ponies or Quarter horses. Where speed and agility are the prime requirements, attention must be paid to the degree of muscling and size of bone, as well as to the soundness of feet and legs. Type differences within the breeds are probably of less importance than between breeds. The statement that horses can have good type and conformation without good performance, but cannot have good performance without good conformation seems to be true.⁹

The various breed-registry associations have definite descriptions as to the ideal type of individual within their breed. Since many breeds of horses are known, a description of each will not be given here. If both type and performance are important, then selection for both should be practiced.

CORRELATIONS BETWEEN TRAITS

Genetic correlations between various traits have not been studied in horses as they have in other classes of farm animals. Some phenotypic

correlations have been studied, however, especially between a trait that can be easily measured and the ability to perform

It has been reported that experienced breeders and handlers of race horses believe that nervous mares, as a general rule, are more likely to produce speedier offspring than are mares that are less nervous or docile. At least, it is thought that the highly spirited horses are usually speedy racers because they have a tremendous will to win in races in competition with others. This has been studied, using 50 high spirited mares that had 272 offspring and 50 phlegmatic mares that had 248 offspring.³ The study showed no significant difference between the average earning indexes of the offspring of the two groups of mares. It was concluded that the temperament of the dam was not correlated with the racing ability of the offspring. It was noted, however, that there was a significant positive correlation between the average earning index of the dam and that of her offspring. This again, demonstrates that racing ability is a heritable trait.

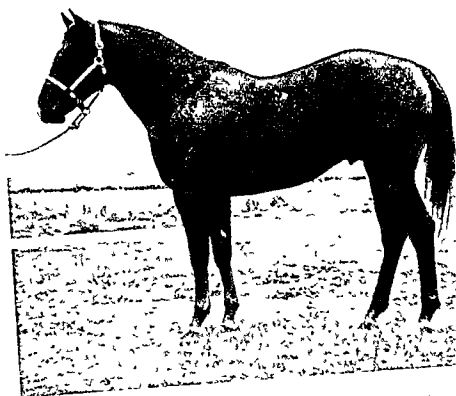
Some breeders of Thoroughbreds believe that coat color is related to racing ability. Leicester, in 1959 made a comprehensive study of such a possible correlation.⁶ The results, based on several hundred horses led to the conclusion that the number of winners of a certain coat color was proportional to the opportunity of horses of that color to win. For example, horses of the chestnut coat color won more races than those that were grey or roan, but this was because more chestnut horses were raced. Another investigator, however, did not agree with these findings and felt that there was a definite correlation between coat color and racing performance.⁷

SELECTION IN HORSES

The existence of several different types and breeds of horses in this country indicates that selection in this species has been effective. One needs only to observe the extreme difference in size between Shetland ponies and draft horses to realize that this is true. Further evidence is found in the various types such as draft horses, pacers, trotters, Quarter horses and Thoroughbreds that have been successfully developed with a definite purpose in mind.

As far as Thoroughbreds are concerned, selection practiced has been based mostly on individuality and/or performance of the parents. Most of the attention has been given to the sire's performance and an attempt has been made to use sires that have been outstanding winners if possible. Better results are obtained when both parents have excellent racing records but even in such matings many of the offspring are disappointing. In one study⁴ it was shown that less than two per cent of the mares studied had an earnings index greater than four. It has also been estimated

FIGURE 84 ALGO, AN EXCELLENT TYPE QUARTER HORSE. HE WAS SHOWN FOR ABOUT TWO AND A HALF YEARS AND WON 52 FIRST PRIZES, 10 GRAND CHAMPIONSHIPS, AND 19 RESERVE GRAND CHAMPIONSHIPS (COURTESY OF THE KING RANCH, KINGSVILLE, TEXAS.)



that 0.05 per cent of the colts registered as a thoroughbred will be good enough to improve the breed.

Selection practiced in Thoroughbreds has been to identify the best and then mate the best to the best. This is still the recommended procedure for best results, as is indicated by the apparently high heritability of racing ability.

In general, mares are not performance-tested as often as are stallions. They also cannot be as superior on the average as stallions because more of them must be kept for breeding, which makes the selection differential smaller. At the King Ranch in Texas, however, attention is given to the selection of mares for "cow sense" and other traits.² The mares are broken and ridden at three, four, and five years of age and are given a chance to show their ability for working cattle. Those that show a good potential and have speed and endurance are checked for soundness, quality, and blood lines. Those that meet the rigid requirements are added to the mare breeding herd. Mares in the breeding herd that fail to produce superior offspring after two or three foals are culled. Such a system of testing and culling should result in progress for the traits of importance, especially in large herds where rigid selection can be practiced.

A pedigree analysis of the Thoroughbred breed was made to determine the degree to which inbreeding has played a part in the improvement and development of this breed.¹⁰ The analysis was made of the pedigrees of stakes winners, losers, and 'millionaire sires,' or those whose offspring have won a million dollars or more in racing. Pedigrees were traced to the year of 1748 as a base for stakes winners and losers in the years 1935, 1940, and 1941. The average inbreeding for 556 stakes winners was 8.23 per cent and that for the losers was 8.00 per cent. Thus, there was little or no difference in the amount of inbreeding in the two groups. It was concluded that the genetic composition of the breed has been influenced very little by inbreeding and linebreeding.

A study of recent pedigrees indicates that, in the Thoroughbred, inbreeding is carefully and purposely avoided. Possibly inbreeding causes a decline in racing ability because of an associated decrease in the stamina and vigor of inbred individuals. Stamina and vigor as well as speed are necessary if horses are to be winners on the track.

An investigation of present day Thoroughbred pedigrees will show that outstanding stallions are often imported from foreign countries and the inheritance of these individuals is mingled with that of superior racing individuals in this country. This is a form of outbreeding and should be of value especially if the imported horses possess some plus genes for racing ability not present in our own racing stock. They should have these genes, for imported horses probably have descended from ancestors different from those of our racing stock at least in the last several years.

Pedigrees of present day Quarter horses will show that some linebreeding and inbreeding is being practiced. Such a pedigree is given in Figure 85. On the other hand there are other pedigrees that show no inbreeding or linebreeding, at least in the three or four generations usually shown. Possibly in those instances in which other traits, such as 'cow sense' and beauty of conformation are bred for, inbreeding and linebreeding may be of more value.

Although inbreeding and linebreeding have been used very little in the development and improvement of some of the present-day breeds, theoretically they could be used to advantage. For instance, linebred families could be formed in which the relationship was kept high to a particular stallion in the breed, with a minimum of inbreeding being involved. If several such distinct families were formed, crossing them might produce a larger proportion of desirable animals in the linecross individuals than is produced by present methods of breeding and selection. Even though individuals in the linebred families might not be outstanding winners themselves they should breed truer than non-inbred parents, and their linecross offspring should show increased heterosis for stamina and vigor. The continued use of linebred families for breeding purposes in a manner comparable to the use of inbred lines of corn could continue to

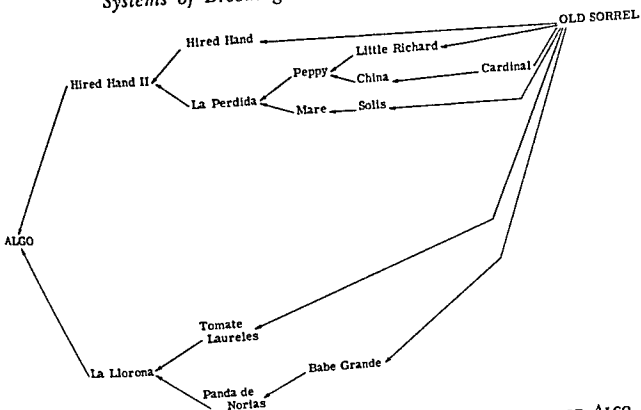


FIGURE 85 ARROW DIAGRAM OF THE PEDIGREE OF ALGO (P-63,952) ILLUSTRATING HOW HE IS LINEBRED TO OLD SORREL.

produce a larger percentage of winners in future years. The same should also be true for gaited animals and Quarter horses. The disadvantage of such a system of mating, however, would be the time and systematic effort required to put it into practice. Whether or not this system of breeding would be profitable, would have to be proved under actual practice.

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Questions and Problems

- 1 Why is breeding efficiency in horses generally low?
- 2 What evidence do we have that indicates that racing ability is highly heritable?
- 3 Is cow sense inherited? Explain
- 4 Are type and performance correlated in horses?
- 5 Outline a breeding and selection program you would suggest to a breeder who wishes to breed outstanding race horses outstanding Quarter horses
- 6 Could linebreeding and inbreeding be used to advantage in improving Thoroughbreds and Quarter horses? Explain

Index

A

- Agammaglobulinemia, 26, 41 42
- Age, cow, effect on milk production, 306 308
- Age, ewe, effect on weaning weight, 289
- Age, parent, influence on offspring, 11
- Albinism, 26
- Alcaptonuria, 25
- Alleles, 36
- Allelomorphs, 36
- Ancon breed, sheep, 8
- Animal breeding, misconceptions about, 10 12
- Artificial insemination, cattle
 - effect on detrimental genes, 264
 - for improvement, 314
 - significance in sire selection, 312
 - testing bulls for use in, 306
- Autosomes, 40
- Average, lifetime, 120

- Breeding stock, selecting, 210
 - accuracy in, 151 152
- Breeding tests for heterozygotes, 128 132
- Butterfat percentage, 305 309
 - correction factor, 308
 - effect of crossbreeding on, 318 319
 - heritability estimate, 305 306
 - and milk yield, 311
 - repeatability estimate, 305 306
 - and yield, 311
- Butterfat production (*see* Milk and butterfat production)
- Butterfat yield, genetic correlation
 - with butterfat percentage, 311
 - with milk yield 311

- Cattle, beef (*cont*)
 improvement program, 276 279
 new breeds, 279 283
- Cattle, dairy
 breeding and selection systems, 303 320
 economic traits, 303 311
- Cell, 14
- Cell membrane, 14
- Certified Meat Hog Program, 139
- Chromosome, 14
- Chromosome aberration, 72, 75 76
- Chromosome number, 14
 abnormalities, 15 16
 reduction, in meiosis, 17 18
 restoration, at fertilization, 22
- Coat color
 effect of epistasis in horses, 46 47
 and racing ability, 328
 selection basis, 136 137
- Coat pattern, 30
- Coefficient of correlation, 103
- Coefficient of variation, 102
- Collateral relatives, selection basis, 142 144
- Commercial livestock production by cross breeding 213
- Commercial pork production, breeding program, 243 244
- Common ancestor, 175
- Comprest Herefords, 261 262
- Consumer tastes, effect on livestock production 4
- Correction factor
 beef cattle, weaning weight
 for age of dam, 256
 for age differences 255
 for sex differences 255
 in breeding programs 211
 butterfat percentage 308
 milk and butterfat production
 for age of cow, 306 308
 for length of lactation period, 306 307
 for milkings per day, 306 309
 sheep weaning weight
 for age 289
 for age of ewe, 289
 swine
 in breeding records 241
 weaning weight, 216 217
 weight at 154 days 217
- Corrective mating, in sheep, 291
- Correlation, genetic, 156 158
 in beef cattle 267
 rate of gain and economy of gain 258
 in dairy cattle, 311 312
 butterfat yield and percentage, 311
 milk yield and butterfat percentage, 311
 milk yield and butterfat yield, 311
 type and milk production, 311
- Correlation, genetic (*cont*)
 estimation, 228
 factor in breeding plans, 211
 in horses, 327 328
 negative, 157-158
 positive, 157
 in sheep, 293 294
 in swine, 228
 use, in selection, 157
- Correlation, phenotypic.
 in beef cattle, 265 267
 in dairy cattle, 311
 in horses, 327-328
- Coupling, 55
- Covariance chart, 184 187
 calculation, 184 186
 calculation of inbreeding coefficient from, 186
 calculation of relationship coefficient from, 186
- Cow pony, 323, 327
- Cow sense, 327 329, 330
- Crossbreeding
 in beef cattle, 268 274
 for commercial livestock production, 213
 in dairy cattle, 319 320
 early experiments, 3
 objections to, 206
 principles 198 207
 in swine
 advantages of, 236
 for commercial pork production, 243 244
 disadvantages of 236
 of non inbred, 233 238
 systems 236-238
 uses of 206
- Crossbreeding effects
 in beef cattle
 on carcass quality, 271 273
 on economy of gain, 270-271
 on fertility, 268
 on rate of gain, 270
 on weaning weight, 269
 in dairy cattle, 317 320
 on butterfat percentage, 318 319
 on milk and butterfat production, 318 319
 genotypic, 198
 phenotypic, 199
 in sheep 294 297
 heterosis, 294 297
 on staple length, 297
 on survival rate, 296
 on weaning weight 297
 on wool weight, 297
 in swine
 with inbred swine, 232
 on sow performance, 235-236

Crossing over, 53-55
 use in chromosome mapping, 55
 Culling, independent, method of inbreeding, 148 149
 Culling during inbreeding, 164
 Cytoplasm, 14

D

Dam genetic contribution to offspring, 23
 Denmark, swine improvement in, 225 227
 Diabetes, 32
 Dickerson, G E, 205
 Dihybrid inheritance, 44 46
 Diploid number, 17
 DNA, significance in inheritance, 25
 Dominance, 35 37
 effect of inbreeding on, 167
 heterotic effect, 200 201
 incomplete, 37 39
 Dwarfism, 28
 in small type beef cattle, 262
 snorter, 29, 263 264

Feeding, swine
 individual, 218
 litter, 218
 to measure economy of gain, 218 219
 Fertility
 in beef cattle, 251 253
 effect of crossbreeding on, 268
 effect of size on, 262
 factors in, 251
 improvement of, 253
 in dairy cattle, 303 304
 effect of inbreeding on, 304, 316
 heritability estimate, 303 304
 repeatability estimate, 303 304
 in horses, heritability estimate, 325
 in sheep, 288 289
 environmental factors in, 288 289
 heritability estimate, 289
 in swine, 215
 Fertilization, 22
 F₁ generation, 45
 F₂ generation, 45
 Finishing ability, steer, and sire size, 261
 First polar body, 21
 genetic correlation

- Gain rate of (*cont*)
 in swine
 and economy of gain 228
 and fatness 228
 gene action affecting 239
 heritability estimate 239
- Galton 155
- Gamma globulin 26
- Gammon Warren 9
- Gene 24 25
 chemical composition 24 25
 locus 24
 monofactorial effects 35 42
 relation to DNA 25
- Gene detrimental 78 89
 in beef cattle 263 264
 in cattle 81 86
 and coat color 80
 in dairy cattle 315
 effect of inbreeding on 315 317
 frequency 79 80
 in horses 87 88
 mode of expression 79
 in sheep 88 294
 in swine 88 89
 time of expression 78 79
- Gene lethal 78 (*see also* Gene detrimental)
- Gene recessive
 effect of inbreeding on dairy cattle 315 317
 physiological effect 166
 selection against by inbreeding 171
 testing for by inbreeding 171
- Gene sublethal 78 (*see also* Gene detrimental)
- Gene action
 chemical nature 25 29
 effect
- Gene action nonadditive
 breeding program for 211
 in dairy cattle 304 306 317
 effect
 on calving interval beef cattle 252
 on economic traits swine 238 239
 factor in heterosis 200
- Gene expression 29 33
 causes of variation in 30 33
 effect of environment on 109 114
 time of 29
 variability in 29 30
- Gene frequencies 65 70
 calculation 67
 effect
 of chance gene fluctuations on 70
 of mutations on 69
 of new alleles on 70
 of selection on 70
 Hardy Weinberg law 66 67
 unaffected by inbreeding 162 163
- Generation interval 156
 effect on selection progress 156
- Genetic defects
 in dairy cattle 315 317
 freedom from importance 263 264
 from mutated genes 25
 (*see also* Gene detrimental)
- Genetic environmental interactions 109 114
 factor in breeding plans 212
 importance to breeder 111 115
- Genetics 7
 misconceptions about 7 10
- Genetic variation 209
- Genotype 36
- Genotypic ratio 37
- Gentry 195
- Gregory H. E. 215

- Heritability estimates (*cont*)
 in beef cattle (*cont*)
 carcass quality, 263
 rate of gain, 257
 in feed regimes, 258
 slaughter grade score, 260
 type score, at weaning, 260
 weaning weight, 254
 in calculating selection progress, 154
 155
 calculation, 115 118
 in dairy cattle
 butterfat percentage, 305 306
 milk and butterfat production, 305
 306
 type, 310
 in horses
 fertility, 325
 racing ability, 325 326
 in sheep
 carcass quality, 291
 face covering, ewe, 293
 fertility, 289
 fleece weight and quality, 293
 nipple number, 298
 rate of gain 289 291
 staple length, 293
 weaning weight, 289
 yearling weight, 291
 in swine
 in calculating selection progress 223
 224
 carcass quality, 239
 conformation, 239
 economy of gain 221
 growth rate, 221
 litter size, 221
 litter weight, 221
 rate of gain, 239
 weight, 154 days 221
 use in selection on basis of phenotype,
 138
- Heterosis (*cont*)
 level, in different crossbreeding systems,
 237
 overdominance a factor in 202 203
 physiological basis, 205 206
 in swine, 240
 traits affected by, 204
 Heterozygosity, 198
 effect of crossbreeding on, 198
 Heterozygote 38
 Heterozygous individual 36
 Hewer, John, 195
 Hewer, William 195
 Holandric inheritance, 40 41
 Homologous chromosomes 14
 Homozygosity
 effect of inbreeding on, 160 162
 effect of linebreeding on, 194
 increased, effect of 163 165
 measurement (*see* Inbreeding measure
 ment)
 Homozygote, 38
 Homozygous individual, 36
 Hormones
 effect on gene expression 32
 pituitary 28 29
 Horses
 breeding and selection systems 324 331
 economic traits 315 327
 Hybrid vigor, 199 (*see also* Heterosis)

- Inbreeding effect of (*cont*)
 - on gene actions 167 170
 - in sheep
 - on staple length 294
 - on vigor 294
 - on wool weight 294
 - in swine
 - on economy of gain 230
 - on growth rate 229
 - on maturity 230
 - on performance 229
 - on sow performance 230
 - on vigor 229
 - Inbreeding coefficient 174
 - calculation 176 180
 - from covariance chart 186 187
 - Inbreeding effects physiological basis 165 167
 - Index average earning 326 328
 - Index equal parent for dairy bulls 312 313
 - Index selection (*see* Selection index)
 - Industrial Revolution 2
 - Inheritance of acquired characters 8
 - role of mutations in 9
 - Inter se* mating 45
 - Litter size swine (*cont*)
 - gene action affecting 238
 - heritability estimate 221 238
 - at weaning 215 216
 - Livestock industry development 13
 - Livestock production 15
 - current changes in 4
 - future of 45
 - improvements in 3
 - requirements for success in 1
 - Longevity beef cattle 265
 - Lush J L 174
- M
- Maternal influence
 - and food utilization swine 228
 - on offspring 11
 - on weaning weight beef calves 254
 - Maternal impressions 78
 - Mating 22
 - Mature equivalent basis for milk yield calculation 307 308
 - Maturity swine
 - and milk production 228
 - effect of inbreeding on 230
 - Mean 98
 - Measurements in breeding programs 211

- Mutation (*cont*)
 - in somatic cells 72
 - use, in study of gene function, 25
- Mutation equilibrium, 69 70
- Mutations accumulated effect on offspring, 11

N

- Neale, P. E., 291
- Nicking ability
 - in swine, 230 232, 237 238
 - testing for, 145
- Nicking effect, 44, 156
 - in dairy cattle, 304
- Nipple number, sheep, 298
- Nucleus 14

O

- Oogenesis, 20
- Oogonium, 20
- "Otter" breed, sheep, 7 8
- Outbreeding
 - grading, 207
 - of horses, 330
 - to produce purebreds, 213
 - topcrossing 206, 207
 - use 206 207
- Ova 17
 - number at mating, 21
- Ovary, 20
- Overdominance 48
 - effect of inbreeding on 167 169
 - heterotic effect 202 203 (*see also* Cross breeding)
- Ovulation, 21 22
- Ovum role in reproduction 13

- Performance testing (*cont*)
 - recommendations for beef cattle, 258 259
 - in sheep, 289
- P_1 generation, 45
- Phenotype, 36
 - selection basis, 136 139
 - variation in, 108
- Phenotypic ratio, 37
- Phenylketonuria, 26
- Pleiotrophic effects, 55
- Pleiotropy, 157
- Polled Herefords, origin 9
- Polydactyly, 73
- Polygenes 44
- Polygenic inheritance, 44
- Polyploidy, 75
- Population
 - definition, 65
 - genetics 65
- Primary oocyte, 21
- Primary spermatocyte, 17-18
- Probability, laws of
 - independent events, 58
 - formula, 61
 - mutually exclusive events 57 58
 - in progeny tests 62 63
 - in recombination of genes 59 60
 - in segregation of genes 58 59
 - use, in breeding tests 129 131
- Probable producing ability, 120
- Productive life span 310
- Progeny test
 - for carcass quality, beef cattle, 262
 - of dairy bulls 312 313
 - future of, 147
 - selection basis 141 147
 - use, in linebreeding 104
- Progeny testing stations swine, Denmark 237 238

Racing ability (*cont*)

- effect of inbreeding on, 330
- heritability estimate, 325 326
- and temperament, 328

Random genetic drift, 70

Random mating, 67

Range, 99

Recessiveness, 35 37

- effect of inbreeding on, 167

Records

- in livestock improvement, 2 4
- in breeding programs 211, 240 242, 256,

Selection (*cont*)

in dairy cattle

- for milk and butterfat production, 305
 - of sires, 312 313
 - for type and conformation, 310
- against dominant gene, 126
- for dominant gene, 126
- effect on gene frequency, 70
- for epistasis, 132 133
- in horses, 328 329
- with incomplete dominance, 39
- independent culling method, 148 149
- methods 147-150

- Selection index (*cont*)
 - for sheep, 298
 - for ewe productivity, 298
 - for weaning weight and face score, 298
 - for wool traits, 298
 - for swine
 - on feeding tests, 223
 - for sow performance, 222 223
 - Selection studies
 - in dairy cattle, 314
 - in sheep, 297 298
 - in swine, 223 225
 - Seminiferous tubules, 17
 - Sex cells, 13
 - formation of, 17 22
 - Sex chromosome, 40 42
 - Sex hormones, 32
 - effect on gene expression, 32
 - Sex influenced inheritance, 42
 - Sex linked inheritance, 40 42
 - Sheep
 - breeding and selection systems, 287 300
 - economic traits 287 293
 - improvement program, 299 300
 - Sickle cell anemia, 27 28
 - Simpson, 195 196
 - Single cross swine, 236 237
 - Sire, genetic contribution to offspring, 23
 - Size of bull
 - and economy of gain of progeny, 261
 - and finishing ability of progeny 261
 - and rate of gain of progeny, 261
 - Slaughter grade, beef cattle
 - and carcass quality, 265 266
 - score, 259 260
 - Snorter dwarfism, 29 263 264
 - Specialization, in livestock production 4
 - Spermatid, 18
 - Spermatogenesis, 17
 - Spermatogonia, 17
 - Spermatozoa 17
 - Swine (*cont*)
 - economic traits, 214 221
 - new breeds, 244 246
 - Synopsis, 54
- T
- Tandem method of selection, 148
 - Telegony, 10
 - Temperament, and racing ability, 328
 - Temperature, effect on gene expression, 31
 - Testes, 17
 - Thoroughbred horses, 324, 326 330
 - effect of inbreeding on, 330
 - selection in, 328 329
 - Three breed cross
 - in dairy cattle, 319
 - in swine, 236 237
 - for commercial pork production, 244
 - Three line cross 172
 - in swine, 230, 232
 - Tomkins, Benjamin, 295
 - Topcross, 206 207
 - in swine 232 233
 - Traits of economic importance (*see* Economic traits)
 - Trotting and pacing ability, 326
 - Twins in genetic environmental studies, 116 117
 - Type
 - in beef cattle 259 262
 - heritability estimate, 310
 - and milk production 311
 - Type score
 - in beef cattle, 259, 260
 - heritability, at weaning 260
 - and rate of gain, 267
 - in swine, 219
 - breeding records 243